# Demography of early life stages of habitat-forming intertidal fucoid algae

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The intertidal zone is finely partitioned in species distributions and abundances. The demographies of key species over varying spatial and temporal scales are fundamental to understanding the population structure and overall dynamics of habitats and assemblages. In this thesis, settlement, dispersal and early life stage survival and growth were examined in several habitat-forming intertidal fucoid algae in New Zealand and Oregon, U.S.A.

Natural settlement patterns of *Hormosira banksii*, *Cystophora torulosa* and *Cystophora scalaris* were quantified for over three years at a semi-protected shore in southern New Zealand. Settlement was monitored in four tidal zones, within bare rock and algal habitats. Settlement was synchronous between tidal zones but the density of settlement varied spatially and temporally. There were significant differences between tidal zones, habitats and times of the year. For *H. banksii*, small pulses of settlement occurred year-round with greatest densities during spring and early summer. Greatest settlement occurred at low tidal zones and under adult canopies. Both *Cystophora* species also reproduced year-round, but had much lower settlement densities than *H. banksii*. Most settlement occurred during spring and summer, while only small pulses occurred in autumn and winter months. Most settlement was in the lowest tidal zone (0.4 m above chart datum), with only a few zygotes settling at higher shore zones. Canopy cover had no significant effect on settlement densities.

Dispersal was examined in *Durvillaea* spp., *H. banksii, C. torulosa* and *Fucus gardneri*. For all species, settlement densities declined with distance from the source populations, but densities were variable between species. *Durvillaea* spp. dispersal was more extensive than expected, with significant settlement occurring 32 m from the source population, the maximum sample range of the study. However, settlement densities were much higher within 8 m from the source. The extensive dispersal of *Durvillaea* spp. is a result of the combination of small, slowly sinking eggs and the presence of buoyant mucilage. The other species studied showed far more restrictive dispersal, and much lower settlement densities. Settlement occurred 2 m from the source, but most settlement occurred under or near the canopy. The eggs of these species are much larger and sink faster than the eggs of *Durvillaea* spp.

The consequences of settling at different shore heights and seasons were examined in *H. banksii* and *D. antarctica* in New Zealand, and *F. gardneri* and *Pelvetiopsis limitata* in Oregon. Transplant experiments tested the effects of grazing and heat/desiccation stress on survival and growth of germlings at different shore heights, during different seasons. High germling mortality was a feature of all species, but rate of mortality depended on conditions and species. There is a trade-off for settling at different times of the year; overall, growth was faster in warmer seasons, but survival was better in cooler seasons. During cooler seasons, germlings are exposed to less heat/desiccation stress, but their slow growth exposes them to grazing and competitive interactions for longer periods. For New Zealand species, shore height had large effects, with better survival and growth in the low shore. Grazers were very effective in the low shore, and heat/desiccation stress had strong effects in the mid and high shores. For Oregon species, effects of grazing and heat/desiccation stress were generally weaker than for New Zealand species. Shore height had weak effects, but ultimately low shore germlings had poor survival, primarily because of overgrowth by ephemeral algae. This is in contrast to the generalisation that survival and growth in the low shore should be better due to a more benign environment.

In this study, species had specific demographies that related to their life history characteristics and responses to the local environment. Differences in settlement, dispersal abilities, survival and growth over small spatial and temporal scales clearly underpinned large scale differences in recruitment and adult distribution and abundances.

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# Chapter 1
# General Introduction

## 1.1 Introduction

Marine algae dominate rocky reefs world-wide, provide habitat and food for a wide range of organisms and are important economic resources. Understanding algal community dynamics is essential in order to manage coastal areas and to predict population recovery and shifts in community structure after environmental disturbance or climate change. This thesis examines the comparative early life stage demography of several habitat-forming fucoid algae. It attempts to explain some of the large-scale differences in distributions and abundances of adults by studying the small scale differences in early life histories. The underlying hypotheses are that profound differences in the early life stages among species affect fundamental processes like dispersal, settlement, survival and growth, and these processes are highly variable over small temporal and spatial scales.

Recruitment limitation is an essential component of community structure models and has been the focus of considerable ecological research. Knowledge about the magnitude and timing of recruitment is fundamental to understanding species distributional limits, replenishment and recovery of populations, and ecological interactions. The notion that recruitment is important in influencing communities has long been recognized but was largely ignored in early research and models (Menge & Farrell 1989, Underwood & Fairweather 1989). Early studies on community structure were mainly descriptive of local-scale and biogeographic patterns of distributions and abundances (Stephenson & Stephenson 1949, Morton & Miller 1968, Ricketts *et al.* 1969, Stephenson & Stephenson 1972). Explanations for the observed patterns were examined experimentally and models focused on the negative structural forces of physical stress, predation and competition (Dayton 1971, Connell 1972, Paine 1974, Dayton 1975, Menge 1976, Menge & Sutherland 1976). Central to this development was the great amount of research on intertidal systems, which encompass a strong gradient of environmental stresses on relatively small spatial scales, and are characterised by abrupt changes in algal and invertebrate abundances. Resident organisms have relatively short generation times compared to terrestrial systems, thereby facilitating the examination of experimental outcomes and recovery from disturbances over short time frames.

One of the strongest paradigms to emerge was that biological interactions, such as competition and grazing, set the lower limits of organisms, while physical variables, such as desiccation, heat or cold stress, set upper limits (Zaneveld 1969, Connell 1972). This paradigm has been widely accepted, but it has also been challenged with alternative hypotheses and experimental evidence, and it is apparent that distributional limits are not as straightforward as previously thought (Chapman 1973, Schonbeck & Norton 1978,

Underwood 1979, 1980, Hawkins & Hartnoll 1983, Underwood & Denley 1984, Underwood & Jernakoff 1984, Hawkins & Hartnoll 1985, Chapman 1986a, Saffo 1987, Chapman & Johnson 1990, Underwood 1991, Chapman 1995, Bertness & Leonard 1997). For example, alternative hypotheses for the upper limits of organisms have considered the lack of supply of propagules or larvae (Underwood & Denley 1984, Underwood 1991), the effects of positive interactions (Bertness & Leonard 1997), and the negative effect of predation (Hay 1979, Underwood 1980). Alternative hypotheses for the lower limits of organisms have included the physiological response to increased immersion (Schonbeck & Norton 1980, Rugg & Norton 1987, Nielsen *et al.* 2006) and the patterns of larval and propagule settlement (Underwood & Denley 1984). It is now widely recognised that species distributions are a result of complex interactions of biological and physical factors that can be highly variable across temporal and spatial scales. One of the biggest challenges facing ecologists is to try and separate these interacting factors to determine which are of primary importance in structuring communities under particular circumstances and conditions.

Broad scale generalizations about the nature and organisation of communities are often controversial and considered to be weak because of the vast differences amongst species and communities (Underwood & Denley 1984, Underwood & Fairweather 1986, Foster & Schiel 1987, Foster 1990, Foster 1991, Underwood 2000). It is essential to repeat experiments with several species over appropriate temporal and spatial scales before generalizations can be applied so that they encompass a range of conditions and reflect broad patterns of organisation. It is also increasingly acknowledged that it is important to examine the microscopic early life stage of organisms to understand the distribution and abundances of adults and ultimately community structure (Underwood & Denley 1984, Underwood & Fairweather 1989, Brawley & Johnson 1991, Underwood 1991, Davison *et al.* 1993, Schiel 2004). A renewal in 'supply-side ecology' has enhanced our knowledge of recruitment limitation in marine systems (Underwood & Fairweather 1989, Underwood 2000).

However, much of the research and subsequent models and theories have only focused on invertebrates, especially mussels and barnacles (Gaines *et al.* 1985, Gaines & Roughgarden 1985, Menge & Sutherland 1987, Roughgarden *et al.* 1988, Menge 1991, Connolly & Roughgarden 1998, Connolly *et al.* 2001). It is difficult to apply such models to algal-dominated shores because algae have very different modes of reproduction, dispersal, and early life stage survival and growth. There are still large gaps in our knowledge of these fundamental characteristics and this information is essential for our understanding of community structure.

### *Early life stages of algae*

The early life stages of algae represent a bottleneck for many species, with massive mortality rates (Santelices 1990, Vadas *et al.* 1992). From the time of release from the parent plant, propagules are affected by a suite of environmental and biological factors that influence their dispersal, settlement and recruitment (see reviews Chapman 1986b, Hoffmann 1987, Santelices 1990, Fletcher & Callow 1992, Norton 1992, Vadas *et al.* 1992, Chapman 1995, Schiel & Foster 2006). These factors can interact and are temporally and spatially variable; consequently, recruitment can be patchy through time and over very small spatial scales. Vadas (1992) described 23 factors influencing the mortality of early life stages of algae, most of which were extrinsic variables. These included the effects of canopy, competition, density, desiccation, grazing, scour, sediment, and water motion. Grazing, canopy and turf effects were identified to be most important, but other, less studied factors such as desiccation and water motion can be significant sources of mortality. Germlings may also exhibit sublethal effects such as reduced photosynthesis and growth, which can increase susceptibility to factors like competition and grazing (Davison *et al.* 1993).

Factors identified as important sources of mortality for the early life stages can also have positive effects. For example, canopies and turfs can enhance settlement and/or survival by trapping propagules and reducing heat and desiccation stress (Brawley & Johnson 1991, Benedetti-Cecchi & Cinelli 1992, van Tamelen *et al.* 1997, Johnson & Brawley 1998, Viejo *et al.* 1999). Grazing can have positive effects by reducing ephemeral algae, thereby enhancing perennial algal recruitment (Lubchenco 1978, Lubchenco & Menge 1978, Lubchenco 1983, Kim 1997, Worm *et al.* 1999, Worm *et al.* 2001). The role of positive interactions in structuring communities has received increased attention in recent years, but most studies have focused on recruit and adult stages of organisms rather than the period from release through to settlement (Bertness & Leonard 1997, Bertness *et al.* 1999, Bertness *et al.* 2002, Lilley & Schiel 2006).

### *Fucoid algae*

Many rocky shores are dominated by fucoid algae and studies worldwide have examined the effects of their removal in an attempt to understand recovery from disturbance and community dynamics (Bertness *et al.* 1999, Jenkins *et al.* 1999, Benedetti-Cecchi *et al.* 2001, Dudgeon & Petraitis 2001, Speidel *et al.* 2001, Bulleri *et al.* 2002, Cervin *et al.* 2004, Cervin *et al.* 2005, Taylor & Schiel 2005, Lilley & Schiel 2006, Schiel 2006). Their presence modifies the environment and facilitates the survival and growth of associated species, and they have been referred to as ‘foundation species’ (Dayton 1973), ‘physical ecosystem engineers’ (Jones et al.

1994, 1997), 'habitat-forming' (Schiel et al. 1995) or 'key species' (Schiel 2006). These seaweeds have simple life cycles (without an alternation of generations), are prolific reproducers and are very abundant. Fertilization, dispersal and attachment usually occur within only a few hours of gamete release (Brawley *et al.* 1999). These characteristics make them ideal species with which to experiment and they have often been used as model organisms for studies of embryogenesis (Bouget *et al.* 2001), reproductive ecology and physiology (Brawley *et al.* 1999).

Dispersal in fucoids is probably relatively short, typically less than 30 m (Sousa 1984, Kendrick & Walker 1991, Chapman 1995, van Tamelen *et al.* 1997, Johnson & Brawley 1998, Dudgeon *et al.* 2001). This is related to their large, negatively buoyant, non-motile eggs. In addition, some species have been shown to release gametes during periods of calm water, and this mechanism may be applicable for fucoids in general (Serrao *et al.* 1996, Pearson & Brawley 1998). The short range dispersal of propagules may be enhanced by the detachment and drift of adults, because many species have buoyant adult plants. Detached plants may drift to distant sites and release gametes; this has been instrumental in the geographic spread of *Sargassum muticum* (Fletcher 1980, Fletcher & Callow 1992). However, this method is considered highly episodic and ineffective for most species (van den Hoek 1987). Dispersal influences species distributions and abundances, genetic structure, recovery and replenishment of populations and ecological interactions. Despite the importance of this fundamental process, information is generally sparse for most species.

Microscopic zygotes and germlings are influenced by a multitude of physical and biological factors before they become macroscopic and recruit to a population. Fucoids are characterized by relatively slow growth which makes them particularly vulnerable to physical stresses, competition and grazing. Microscopic stages are difficult to study, especially in field experiments, and most information on factors contributing to early life stage survival has come from studies of recruitment. Information on the microscopic early life stage is lacking for many fucoid species (Chapman 1995, Schiel & Foster 2006).

Fucoid life history characteristics are fundamentally very different and this influences their reproduction, dispersal, settlement and recruitment. Species that appear to be functionally and morphologically similar can have intrinsic differences in life history characteristics which affect their responses to the biological and physical environment. For example, species are either monoecious or dioecious and this has ramifications for fertilization success and the genetic structure of populations (Brawley & Johnson 1992). Reproductive periodicity varies considerably among species (Hoffmann 1987, Brawley & Johnson 1992); some are reproductive year-round while others are seasonally constrained,

which influences succession events and competitive interactions. Gamete release can depend on the tidal cycle; some intertidal species release gametes during high tide, but others release during low tide which may reduce dispersal (Johnson & Brawley 1998). Most species release gametes into the surrounding environment but many species, including those of *Sargassum* and *Cystoseira* retain zygotes on the adult plants for several days until they are well developed gemlings (Dawson 1941, Fletcher 1980, Schiel 1985). This affects propagule dispersal because germlings are large and sink fast when released, resulting in highly localised settlement patterns (Kendrick & Walker 1991, 1995). Differences in sizes of propagules and germlings between species also affect post-settlement interactions because larger sizes may have competitive advantages and refuges from grazing. Information about the details of life history characteristics is essential to understand species survival and growth, and ultimately allow insight into how algal communities are structured.

## 1.2 Study Aims

This thesis tests hypotheses about the spatial and temporal variability in dispersal, settlement and early life stage survival and growth on the recruitment of habitat-forming intertidal fucoid algae. These are critical stages in the successful establishment of marine algae, and information on the processes affecting them is essential for understanding adult distributions and abundances, the connectivity, replenishment and recovery of populations, ecological interactions and community structure. The majority of this study was carried out in New Zealand on *Hormosira banksii*, *Durvillaea antarctica*, and *Cystophora* spp. Some reciprocal experiments on *Fucus gardneri* and *Pelvetiopsis limitata* in Oregon, U.S.A. allowed inter-hemispheric comparisons of early life stage demography.

The species examined, although common and wide-ranging, have specific adult distributions and niches. Some have narrow distributions, located only in specific wave exposures and tidal zones, and appear to be highly adapted for their habitat. Others have broad distributions, found across tidal zones and wave exposures. For example, *D. antarctica* is found only at wave exposed sites, on the low shore. In contrast, *F. gardneri* is found in sheltered and exposed sites, from the high to low shore. Reasons for the distinct distributions and abundances of adults are not intuitively obvious. It is unknown whether a lack of supply, post settlement mortality, or a combination of both set these limits. This study examines dispersal and the early life stage survival between species to investigate whether, even at this microscopic stage, species have intrinsic responses to interactions with the physical and biological environment.

Chapter 2 identifies the large spatial and temporal variation that occurs in settlement patterns. This information highlights the variability in reproductive cycles and output between species, and small-scale differences in settlement. Chapter 3 examines eggs sizes, sinking rates and dispersal distances. The information from these two chapters is used to develop hypotheses about the consequences of this variable settlement on the survival and growth of the early life stages. These are experimentally evaluated by testing the effects of grazing and heat stress/desiccation on the survival and growth of transplanted germlings across shore heights (Chapter 4). Specific questions and hypotheses are outlined in each chapter.

### 1.3 Study areas

Sites in New Zealand were on the east coast of the South Island of New Zealand, on and near the Kaikoura Peninsula (Fig. 1.1; 42° 25' S, 173° 44' E). The Kaikoura Peninsula has large intertidal platforms composed of mudstone and limestone. South of the Peninsula, the intertidal reefs are composed of greywacke. Kaikoura is unique in its geography in that the continental shelf is only 4-5 km from the shoreline, and depths of over 2300 m occur approximately 20 km southeast of the Peninsula (Rasmussen 1965). The coastline is subjected to strong wave action and oceanic swells resulting from winds that are predominately south and southeast in winter, and northeast in summer (Rasmussen 1965). However, many of the intertidal platforms are sheltered due to their aspect and the presence of offshore outcrops. Water temperatures range between 9-18˚C (Chiswell & Schiel 2001). Several rivers are located to the north and south of the Peninsula and contribute significant amounts of sediment to the nearshore water mass, especially during flooding.

Sites in Oregon were at Fogarty Creek (44° 51' N, 124° 03' W) and Depoe Bay (44° 48' N, 124° 03' W), approximately 30 km north of Newport (Fig. 1.2). These sites are basaltic, exposed platforms that are separated by approximately 3.5 km. Offshore waters are influenced by the California Current which consists of cold, southward flowing water (Roughgarden *et al.* 1988). Central Oregon nearshore waters are characterized by weak intermittent upwelling and relaxation events (Connolly & Roughgarden 1998). Specific sites are described in more detail in each chapter.

New Zealand and Oregon are at roughly the same latitude, have long stretches of rocky intertidal shores and an abundance of fucoid seaweeds. However, their tidal regimes are very different. In New Zealand the tides are semidiurnal and are of equal magnitude. In Oregon, the tides are mixed semidiurnal, with different amplitudes. High-high and low-low tides are followed by low-high and high-low tides. During summer the low-low tides can occur during the day, which can exert tremendous stresses on the intertidal communities because they are emmersed for very long periods. During winter, the low-low tides occur during the night.

Intertidal community structures are also quite different between the two study areas. In New Zealand, the sites have high shores dominated by bare space and grazers, with some ephemeral algae. Perennial algae are restricted to the mid and low shore. *H. banksii* is the only midlittoral fucoid, and is associated with an understorey of coralline algae. It dominates the mid to low shore of sheltered sites (Fig. 1.3). The low shore and immediate subtidal are dominated by *Cystophora* spp. in sheltered situations, and by *Durvillaea* spp. at exposed sites (Fig. 1.4). A diverse number of grazers are present, with several species of limpets, chitons,

turbinids and trochids. In contrast, Oregon has a many perennial seaweed species in the high shore, including the fucoids *Pelvetiopsis limitata* and *Fucus gardneri* (Fig. 1.5 and 1.6). The mid shores are dominated by mussels and barnacles, and algae dominate the low shore. Low shore algae include several species of red algae and small patches of *F. gardneri*. Grazers are very abundant throughout the tidal range, but are represented by far fewer species. Limpets of the genus *Lottia*, and littorines are highly abundant, and the trochid *Tegula funebralis* is present in high shore sheltered areas.

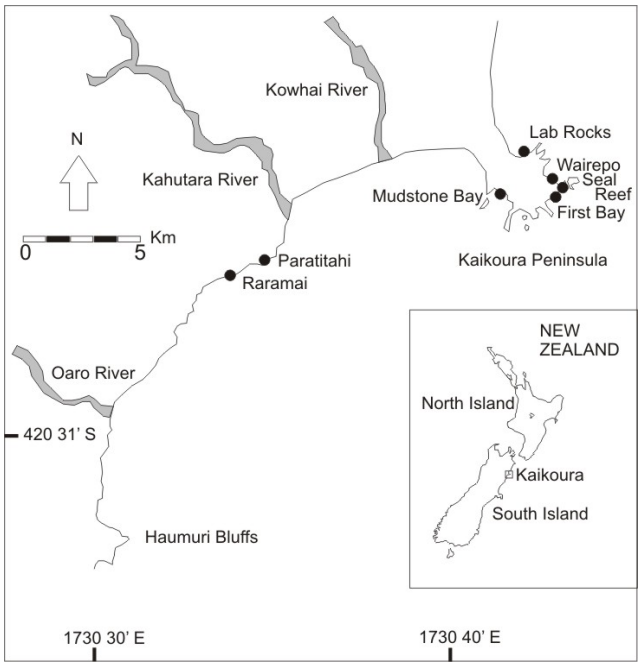


**Figure 1.1** Map of Kaikoura Peninsula showing study sites and location within New Zealand.

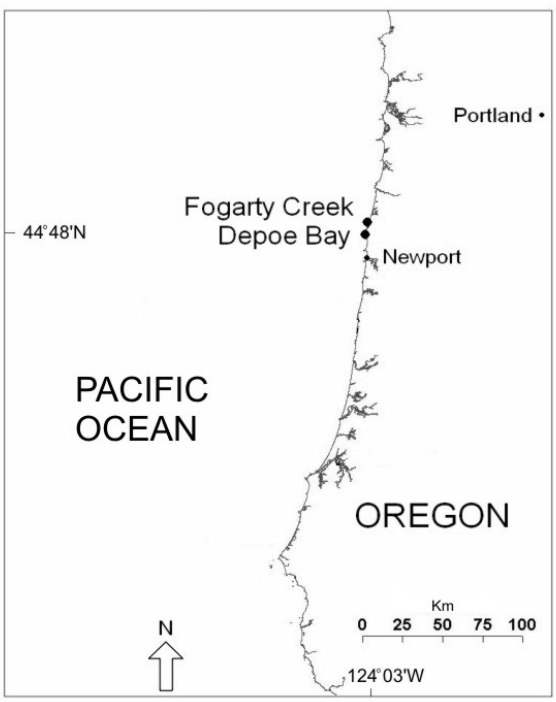


**Figure 1.2** Map showing study sites in Oregon, U.S.A..

**Figure 1.3** Wairepo, New Zealand. Semi-sheltered site, with the high shore dominated by bare space and grazers, mid shore and low shores dominated by *H. banksii* and *Cystophora* spp. respectively, with an understorey of coralline algae. High to low tide is approximately 150 m.

**Figure 1.4** Seal Reef, New Zealand. Exposed site with an extensive high shore dominated by bare space, grazers, and some ephemeral algae, mid shore cracks and crevices dominated by *H. banksii*, low shore dominated by *Durvillaea* spp. Algal zones have an understorey of coralline algae. High to low tide is approximately 60 m

**Figure 1.5** Fogarty Creek, Oregon. High shore dominated by several perennial algae and barnacles (including *F. gardneri* and *P. limitata*), mid shore dominated by mussels and barnacles, low shore dominated by algae. High to low tide is approximately 50 m.

**Figure 1.6** Depoe Bay, Oregon. Distinct zonation pattern: low shore dominated by algae and seagrass, mid shore dominated by mussels and barnacles, and high shore dominated by barnacles and algae. High to low tide is approximately 15 m.

## 1.4 Study species

### *Hormosira banksii*

*Hormosira banksii* (Turner) Descaisne, or Neptune's Necklace, is common throughout New Zealand, and is also found in southern and eastern Australia. It dominates many semi-sheltered reefs, and is found in lower abundances in sheltered habitats at more exposed sites. It is distributed from mid to low tide and also inhabits tide pools. Plants grow up to 50 cm, and their morphology is adapted for withstanding heat and desiccation stress by having thick-walled, fluid-filled bladders or 'nodes', which are also buoyant (Morton & Miller 1968) (Fig. 1.7). *H. banksii* is dioecious and can often be observed releasing gametes at low tide. Plants are fertile year-round (Osborn 1948) and gametes are produced in conceptacles located on the entire surface of the thallus node. Four eggs are produced per oogonium.

Many algae and invertebrates depend on the presence of *H. banksii* (Lilley 2004, Lilley & Schiel 2006, Schiel 2006). An epiphytic fucoid, *Notheia anomala*, is found exclusively on *H. banksii*. *Corallina officinalis*, an encrusting and turfing (non-geniculate and geniculate) understorey coralline alga associated with *H. banksii*, is 'bleached' and die-back occurs when the fucoid canopy is removed. Many other algal and invertebrate species also disappear or become severely reduced in abundance with canopy removal (Lilley 2004, Lilley & Schiel 2006, Schiel 2006).

### *Durvillaea antarctica* and *D. willana*

*Durvillaea antarctica* (Chamisso) Hariot, or bull kelp, is common throughout New Zealand and is also found at the Subantarctic Islands and Chile. In contrast to *H. banksii*, it is found only on exposed reefs. It occurs on the low tide fringe, and grows up to 10 m long (Adams 1994) (Fig. 1.8). Plants have large holdfasts and flexible stipes which allow them to withstand the forces of large waves. The blades are thick and leathery and have a honeycomb structure inside which causes the plants to be buoyant. Conceptacles are located on the entire blade surface, except in areas of new growth on blade edges. Plants are dioecious, releasing eggs (in packets of four) and sperm with sticky mucilage at low tide (Naylor 1953). Plants are reproductive during autumn – early spring (Naylor 1953, Hay 1977, Collantes *et al.* 2002). Usually only encrusting coralline algae are found underneath *D. antarctica*, and little else due to the whiplash effect of the fronds (Taylor & Schiel 2005). A specialized fauna of limpets, chitons, worms and crustaceans inhabit the holdfasts (Morton & Miller 1968).

*Durvillaea willana* Lindauaer is found in southern Australia and southern New Zealand on exposed coasts. Its vertical distribution is limited to the immediate subtidal, below the *D. antarctica* zone. It grows to 5 m, has lateral branches on its stipe, and blades lack a

honeycomb structure so plants are not buoyant (Morton & Miller 1968, Adams 1994). Plants are dioecious and are reproductive during autumn – early spring (Naylor 1953).

***Cystophora torulosa* and *C. scalaris***

*Cystophora torulosa* (R. Brown ex Turner) J. Agardh and *Cystophora scalaris* J. Agardh are found in New Zealand and south eastern Australia (Fig. 1.9).They are abundant on semi-sheltered reefs, in the low shore to immediate subtidal. *C. torulosa* grows slightly higher on the shore than *C. scalaris*. Plants grow to approximately 1 m (Adams 1994). In contrast to *H. banksii* and *D. antarctica*, these species are monoecious, and one egg is produced per oogonium. Plants have a long main axis from which lateral branches arise, and receptacles are located at the end of the latter (Adams 1994). Buoyancy is achieved by vesicles positioned on the lateral branches.

***Fucus gardneri***

*Fucus gardneri* P.C. Silva (formerly *F. distichus*) is distributed in the northern Pacific, from California to Alaska, U.S.A. Plants are usually 10-25 cm tall (Abbott & Hollenberg 1976) and at our sites in Oregon were most abundant on the high shore, but were also found in lesser abundances on the low shore (Fig. 1.10). Reproductive plants are present year-round but peak reproduction is dependent on location, with peaks reported in autumn and winter in Canada (Ang 1991), and summer in Washington (Thom 1983). Plants are monoecious, and produce 4 eggs per oogonium (Fritsch 1945, Serrao *et al.* 1999). Eggs are produced in conceptacles which are borne on mucus-filled receptacles on tips of thalli (Fritsch 1945). Gametes are released in conjunction with copious amounts of viscous mucilage. This mucilage has several effects; it reduces desiccation and can carry gametes to the understorey which is cool and damp, thereby reducing dispersal because eggs are introduced to the substratum before the incoming tide can carry them away (Brawley & Johnson 1992, Brawley *et al.* 1999). It may also reduce self-fertilization because a critical viscosity of the mucilage is required for successful fertilization to occur (Pollock 1969). This viscosity is achieved by dilution of the mucus with seawater. Recruitment of *F. gardneri* is enhanced by barnacles, which reduce heat, desiccation and grazing stress (Kim 1997, van Tamelen & Stekoll 1997).

***Pelvetiopsis limitata***

*Pelvetiopsis limitata* (Setchell) N.L. Gardner has a distributional range from California, U.S.A., to British Columbia, Canada. It is found exclusively on the high shore, and grows 4-8 cm tall (Abbott & Hollenberg 1976)(Fig.1.11). It appears to be highly resistant to desiccation since during low-low tides followed by low-high tides, the plants can be exposed for extremely long periods without mortality. It is monoecious, and produces one egg per oogonium (Fritsch 1945, Serrao *et al.* 1999). Recruitment of *P. limitata* is facilitated by the

presence of barnacles providing refuges from grazing from the numerous limpets and littorines that inhabit their zone (Farrell 1991)

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**Figure 1.7** *Hormosira banksii* male plant releasing orange sperm (above) and female plant releasing brown eggs (below). Dominates mid-low shore semi-sheltered sites in New Zealand.

**Figure 1.8** *Durvillaea antarctica* and *D. willana* in the low shore at an exposed site, Seal Reef, in New Zealand.

**Figure 1.9** *Cystophora scalaris* (left) and *C. torulosa* (right), low shore species that dominate semi-sheltered areas in New Zealand.

**Figure 1.10** *Fucus gardneri*; frond tips are mucus-filled and are covered in conceptacles. Abundant in the high shore, but also found lower on the shore in Oregon, U.S.A.

**Figure 1.11** *Pelvetiopsis limitata*; an extremely hardy high shore species that is very resistant to desiccation. Frond tips contain conceptacles. Restricted to the high shore in Oregon, U.S.A.

# Chapter 2
# Spatial and temporal variation in settlement

## 2.1 Introduction

A major criticism of early models of intertidal community structure has been that they do not take into account variability in larval or propagule supply (Underwood and Denley 1984, Menge and Sutherland 1987, Menge 1991). Instead, in these models, distributions and abundances of species are explained by post-settlement community interactions with the physical environment (Connell 1975, Menge 1976, Menge and Sutherland 1976). Underwood and Denley (1984) proposed that variation in settlement and recruitment will alter the intensity and outcome of interactions (such as predation and competition), thereby affecting community structure. Subsequent studies have attempted to quantify propagule supply and/or settlement rates (Hoffmann and Ugarte 1985, Zechman and Mathieson 1985, Minchinton and Scheilberg 1991, Pearson and Brawley 1996, Walters and Wethey 1996, van-Tamelen et al. 1997), and have identified settlement patterns as important factors in determining community structure (Gaines et al. 1985, Gaines and Roughgarden 1985, Underwood and Fairweather 1989, Menge 1991, Connolly et al. 2001). However, with the exception of studies on barnacles and mussels (see Raimondi 1990 and references therein), there remains a lack of basic data on the reproductive periodicity, settlement and recruitment of many common and ecologically important species. In addition, much of the information we have is from short-term studies (often from single sites) which do not take into account reproductive periodicity, between site variation, and the local-scale patchiness of habitats.

Settlement patterns of marine organisms have been shown to vary tremendously both spatially and temporally (Hruby and Norton 1979, Caffey 1985, Connell 1985, Raimondi 1990) (and see reviews Hoffmann 1987, Santelices 1990). In marine algae, spatial variability in settlement is the result of many factors, but is largely dependent on the dispersal potential of the species (Hoffmann 1987, Santelices 1990). In contrast to many invertebrates, most algae have limited dispersal with no obligate planktonic period. The extent of dispersal is influenced by the characteristics of the parent plant, egg, spore or zygote, environmental conditions at the time of gamete release (e.g. waves, currents etc.), topography of the shore and the presence of large algae that can modify water currents (Hoffmann 1987, Santelices 1990, Chapman 1995). Spatial variation in settlement is also influenced by the size and fecundity of the source population. A large adult population with high fecundity can have a higher dispersal potential, and a greater spore shadow, than a smaller population with low fecundity due to the effects of dilution and diffusion (Anderson and North 1966, Hoffmann 1987, Norton 1992, Reed et al. 1997, Reed et al. 2004).

A consequence of limited dispersal, a trait of many algae, is that most propagules settle within or at the edge of adult stands (Reed et al. 1988, Kendrick and Walker 1995,

Johnson and Brawley 1998). Johnson and Brawley (1998) found that settlement of *Pelvetia compressa* was 1-2 orders of magnitude greater under than outside an adult canopy. Kendrick and Walker (1995) determined that most propagules of *Sargassum* spp. settled within the bed from which they originated, with 98% of propagules settling within 1m of their parent plant. These dispersal patterns are similar to those of terrestrial plants, with an inverse relationship between settlement density and distance from the source plants (Howe and Smallwood 1982).

Algal canopies can have positive and negative effects on settlement and recruitment (Vadas et al. 1992). Canopies can protect propagules from heat and desiccation (Brawley and Johnson 1991, van-Tamelen et al. 1997, Viejo et al. 1999) and modify water currents by slowing the flow and facilitating settlement during propagule release (Santelices 1990). However, the presence of a canopy can also form a physical barrier to prevent settlement (Dayton 1973, Deysher and Norton 1982) or decrease penetrable light thereby inhibiting or slowing germination, photosynthesis and growth (Dayton et al. 1984, Reed and Foster 1984, Davison et al. 1993, Jenkins et al. 1999). Adult plants can also detach germlings by sweeping (Santelices and Ojeda 1984, van-Tamelen et al. 1997). Also, their presence can lead to greater mortality by increasing the duration of foraging by grazers by keeping the understorey cool and damp (Johnson and Brawley 1998). Consequently, the presence of adult plants can cause considerable spatial variation in settlement and recruitment of algal propagules.

Temporal variation in settlement is often attributed to the life history traits of the species, and combined with periodic disturbances can have profound effects on community structure. Some species are reproductive for large parts of the year (usually early successional or opportunistic species), while others have more restricted and seasonal reproductive periods (usually late successional species) (Sousa 1979, Santelices 1990). Species that reproduce throughout the year maximize their recruitment success because favourable settlement and recruitment windows can be highly variable in time and space (Deysher and Dean 1986, Reed et al. 1988). Following disturbance, the species that recruits first often becomes the dominant space-occupier affecting subsequent successional processes (Sousa 1979, Sousa et al. 1981). Small differences in the time of disturbance can, therefore, lead to a profound disparity in the species which come to occupy space simply due to the timing of reproduction in potential space occupiers.

The environmental conditions during reproductive periods are also very important in influencing gamete release and subsequent settlement of fucoid algae. Cues for gamete release have been related to hydrodynamic conditions (Serrao et al. 1996, Pearson et al. 1998), light (Togashi and Cox 2001), temperature (Rao and Kaliaperumal 1987), lunar and/or tidal cycles (Andersson et al. 1994, Togashi and Cox 2001), and combinations of the above. Synchrony of

gamete release is important because it increases gamete concentration, which enhances fertilization (Brawley and Johnson 1992, Reed et al. 1997). It also increases the dispersal potential of propagules by increasing the concentration of fertilized propagules at their source, which ultimately influences the density of settlement (Anderson and North 1966, Hoffmann 1987, Norton 1992, Reed et al. 1997, Reed et al. 2004).

Many subtidal and intertidal communities are dominated by algae that provide habitat and/or food for numerous invertebrates, fish and other algae. They have been referred to as 'physical ecosystem engineers' (Jones et al. 1994, 1997), 'foundation species' (Dayton 1973), 'habitat-forming' (Schiel et al. 1995) or 'key species' (Schiel 2006) because their presence modifies the environment and facilitates the survival of associated species. Fucoid algae are important habitat-formers on many rocky intertidal shores worldwide, yet little is known about variation in their propagule supply and settlement patterns. In the fucoid life cycle a diploid adult produces haploid eggs and spermatozoids which, following fertilisation, develop directly into diploid juveniles which grow into adult thalli. There is no alternation of generations. This relatively simple life cycle facilitates the testing of components of community structure models that relate to propagule supply and variability of settlement (Chapman 1995, Johnson and Brawley 1998). Furthermore, fucoid eggs are relatively large, dense and non-motile (Chapman 1995). Their limited dispersal potential (Kendrick and Walker 1995, Johnson and Brawley 1998) allows for fine-scale studies of variation in settlement and dispersal from known source populations.

This chapter examines spatial and temporal variation in settlement of several New Zealand habitat-forming fucalean species. It investigates the effect of site, shore height, and habitat on settlement through time. In southern New Zealand, distinct zonation patterns separate fucoid species on semi-sheltered intertidal platforms. *Hormosira banksii* is dioecious and is the only midlittoral fucoid, forming dense canopies from mid to low shore (Morton and Miller 1968). *Cystophora torulosa* and *Cystophora scalaris* are monoecious fucoids which form a distinct band downshore from the *H. banksii* zone. Patches of bare rock (ranging in size from tens of centimetres to several meters in diameter) are prevalent within these algal-dominated zones, and the recruitment of fucalean algae is never observed in these bare patches. A long-term experiment tests the hypothesis that bare patches within these fucoid stands are caused by a lack of propagule supply (recruitment limitation), and examines variation in the initial supply of algal propagules between habitats, zones and through time. This experiment also defines reproductive periodicity by measuring settlement rates and identifies any synchrony between shore heights and between species. In a shorter-term experiment, the variation in *H. banksii* settlement between sites examines synchrony in the magnitude and timing of settlement, and

ascertains if the size of the adult population affects the amount of settlement. The sites ranged from having large stands of adults several hundred square metres in area, to small patches only a few square metres in area.

## 2.2 Methods

### 2.2.1. Experimental substrate

All settlement experiments used artificial plates because they provided a standard substrate on which the microscopic germlings could be distinguished. Initial trials using both fibrolite ('Hardiflex™') and concrete plates showed fibrolite was a superior settlement surface and subsequently only this was used (Dunmore and Schiel, unpublished data). The square fibrolite plates were 11 x 11 cm and 7 mm thick. Plates had a hole in the centre to enable attachment to the substratum by a stainless steel screw that was inserted into a plastic Rawl plug in the rock. Plates were recessed into the rock to ensure they were flush with the substratum. Stainless steel mesh fences were used to exclude grazers. The fences were 11 x 11 cm and 4 cm high, with a 2 cm lip at the top. The mesh had holes 2 x 2mm. A pilot experiment showed that the fences had no significant effect on the density of algal settlement (ANOVA results: $p=0.352243$). To monitor algal settlement, a microscope was used to count algal propagules in five haphazardly chosen 1 $cm^2$ areas on each plate. To minimize possible edge effects, a 1 cm margin around the edge of each plate was excluded. Many different algal species settled on the plates, but *H. banksii* and *Cystophora* spp. were easily distinguished. The *Cystophora* spp. could not be identified to species level and were a mixture of *C. torulosa* and *C. scalaris*.

### 2.2.2. Settlement of *Hormosira banksii* and *Cystophora* spp. between shore zones and habitats

This experiment examines the variation in settlement between habitats and shore zones through time. The study site was at Wairepo, on the east coast of the South Island, New Zealand (42° 25' S, 173° 42' E; Fig.2.1). Wairepo is a semi-sheltered siltstone platform located on the Kaikoura Peninsula. The platform is gently sloping and extends approximately 150m from the low- to high-tide marks and is several hundred meters wide. The vertical zonation of the reef is characterised by distinct changes in algal composition and abundance. Four separate zones were identified. The 'low *Cystophora* zone' (LCZ), extending from 0.2 – 0.5 m above chart datum, was dominated by *C. torulosa* and *C. scalaris*, and had small (<100$cm^2$) patches of *H. banksii* present. The 'low *Hormosira* zone' (LHZ), from 0.5 – 0.9 m above chart datum, had dense canopies of large *H. banksii* plants (average sum of frond lengths of 60 random adult plants = 601cm +/- 46.3 s.e.). The 'mid *Hormosira* zone' (MHZ), from 0.9 – 1.1 m above chart datum, was also dominated by *H. banksii*, but the plants were

smaller (average sum of frond lengths of 60 random adult plants = 450 cm +/- 37.9 s.e.). The underlying substrate of both the mid and low shores was a mixture of encrusting and turfing coralline algae, and small amounts of bare substratum. Finally, the 'high bare zone' (HBZ), from 1.0 to 1.7 m above chart datum, was bare of macroalgae. Two distinct habitats were defined within the two *H. banksii* zones. The first was *H. banksii* plants with an understorey of coralline algae. The second was bare rock patches interspersed within algal areas and dominated by grazers.

Plates were placed in the four distinct zones described above (0.4, 0.8, 1.0 and 1.1 m above chart datum in the LCZ, LHZ, MHZ and HBZ respectively). Plates in the LCZ were placed under a *C. torulosa* canopy (n=3), and within canopy clearances of the same size as the plates (121 $cm^2$) (n=3). Plates in the two '*Hormosira* zones' were placed within bare rock patches (n=3), under *H. banksii* canopy (n=3), and within canopy clearances of the same size as the plates (121 $cm^2$) (n=3). Plates in the high zone could be placed only in the bare rock habitat. Plates were placed in their respective habitats for a duration of 1 week, twice a month. The study ran from September 1998 until January 2002. The weeks of placement were randomly chosen. Plates were not placed in the *Cystophora* zone until January 1999.

Daily settlement was assessed during four intervals (April and May 2000 in the MHZ and LHZ, and in September and October 2002 in the LHZ) to determine if daily patterns were similar to weekly patterns. During these intervals, twice the number of plates (n=6) were placed on the shore. Half were collected after 24 hours and the rest were collected after 1 week.

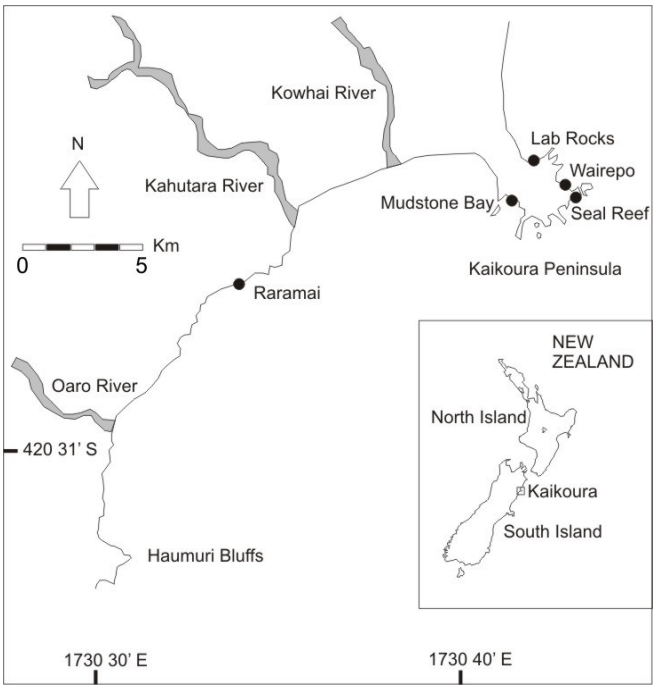


**Figure 2.1.** Map of Kaikoura Peninsula showing study sites and location within New Zealand.

### 2.2.3. Settlement of *Hormosira banksii* between sites

This experiment tests for any synchrony of settlement between sites separated by 1 - 15kms, and determines whether the size of the adult population affects the amount of settlement. The 5 sites used had different sized areas of *H. banksii* populations, and were located on and to the south of Kaikoura Peninsula (Fig. 2.1). Table 2.1 shows the percent covers within areas populated by *H. banksii* at each site. Wairepo, Mudstone Bay and Lab Rocks are semi-sheltered. Wairepo is described above and has the largest algal population. Mudstone Bay (42° 25' S, 173° 41' E; Fig. 2.1) and Lab Rocks (42° 24' S, 173° 41' E; Fig. 2.1) are smaller reefs, extending only 50 meters from the low to high tide marks. Seal Reef (42° 25' S, 173° 43' E; Fig.2.1) and Raramai (42° 27' S, 173° 33' E; Fig.2.1) are exposed sites and have small *H. banksii* populations. Plates were placed in the low shore, within canopy clearances the size of the plates. Plates were placed in the low *Hormosira* zone (approximately 0.8 m above chart datum) for 1-week periods, 13 times between October 2001 and February 2002.

**Table 2.1.** Percent covers and total areas of *H.banksii* populations in the low *H. banksii* zone at each site.

| Site | % cover of *H. banksii* (average of five 0.25 $m^2$ quadrats) | Area of *H.banksii* population |
|---|---|---|
| Wairepo | 100 (+/- 0.2 s.e.) | >100 $m^2$ |
| Mudstone Bay | 64 (+/- 9 s.e.) | ~50 $m^2$ |
| Lab Rocks | 89 (+/- 3 s.e.) | ~50 $m^2$ |
| Seal Reef | 44 (+/- 9 s.e.) | ~4 $m^2$ |
| Raramai | 53 (+/- 8 s.e.) | ~4 $m^2$ |

### 2.2.4. Data Analysis

Data testing the effect of shore zone and time, and that of habitat were analysed separately because not all habitats were present at each shore height. Both analyses used general linear models of analysis of variance. The effects of shore zone, year, season, month and week on settlement were analysed using a hierarchical model and nested season within year, month within season and week within month. To eliminate canopy effects, only data from the plates outside adult canopies in the *Hormosira* and *Cystophora* zones, and the plates in the high bare zone were used. The second model tested the effect of habitat. This analysis only used data from the monitoring periods that had settlement. For *H. banksii* settlement, data from the *Hormosira* and *Cystophora* zones were analysed separately. Analysis of *Cystophora* spp. settlement used only data from the *Cystophora* zone because little settlement occurred in higher zones. For both models, week was treated as a random factor. Prior to ANOVA, homogeneity of variances were checked using Cochran's tests and data were log transformed where necessary. If variances could not be stabilised, more conservative p-values were used.

Statistica 7 (Copyright© StatSoft Inc.) was used in all analyses.

Settlement through time was graphed to illustrate an annual cycle for both *H. banksii* and *Cystophora* spp. Cummulative annual settlement in each habitat was plotted for *H. banksii* and *Cystophora* spp. in the *Hormosira* and *Cystophora* zones. Daily versus weekly settlement was analysed using ANOVA, testing the effect of duration and habitat on settlement. Synchrony of *H. banksii* settlement between different shore heights and different sites was tested using correlation analyses. Correlation analysis was also used to test for any association between monthly average settlement and average temperature, and between monthly average settlement and southern oscillation index values.

## 2.3. Results

### 2.3.1. *Hormosira banksii* and *Cystophora* spp. settlement between shore zones and habitats

***Hormosira banksii***

*H. banksii* settlement occurred throughout the year and was highly synchronous between zones, but the intensity of settlement often varied by two orders of magnitude across zones. For example, settlement in December 1998 was 560 (s.e. 397) $cm^{-2}$ in the LHZ, 130 (s.e. 130) $cm^{-2}$ in the MHZ; and 5 (s.e. 7) $cm^{-2}$ in the HBZ (Fig. 2.2, Table 2.2). Overall, the greatest settlement occurred in the LHZ, followed by the MHZ, the LCZ and the HBZ (Fig. 2.2, Table 2.3.). Most settlement occurred during spring and early summer (September – January) (Table 2.3.), with a maximum average settlement of 1518 (s.e. 679) $cm^{-2}$ in the LHZ in December 1998. There was a significant season (within year) x zone interaction because although summer and spring almost always had greater settlement than the other seasons, this was not as pronounced in the high zone. Furthermore, in some seasons there was greater settlement in the LHZ, and in other seasons settlement was greater in the LCZ. Reduced, or no settlement occurred during late summer and winter. Settlement within each zone differed between weeks, between each month of the year, and between seasons (Table 2.3.). Low or no settlement usually followed high settlement (Fig 2.2). Overall, settlement was not significantly different between years, but settlement in 2000 was higher in the spring and summer than in the other years (c.f. mean *H. banksii* per $cm^2$ in spring and summer respectively: 41 and 63 in 2000, 20 and 45 in 1999, and 14 and 17 in 2001). There were no correlations between monthly average settlement and monthly average air temperature or SOI values, but there were significant correlations ($p<0.05$) between settlement and 3-month running averages of the SOI values (Fig. 2.2).

**Table 2.2.** Correlation matrix of *Hormosira banksii* settlement between zones. ($r_{72}$= 0.375; p<0.001***)

| | High Bare Zone | Mid *Hormosira* Zone | Low *Hormosira* Zone |
|---|---|---|---|
| Mid *Hormosira* Zone | 0.63*** | | |
| Low *Hormosira* Zone | 0.56*** | 0.81*** | |
| Low *Cystophora* Zone | 0.49*** | 0.40*** | 0.61*** |

*H. banksii* settlement was greatest under the canopy (Fig. 2.3, Table 2.4.). In the LHZ, lowest settlement was in the bare habitat and intermediate settlement densities occurred where the canopy had been removed. This pattern was less clear in the MHZ; more settlement occurred under a canopy, but there was no difference in settlement in bare areas and areas with the canopy removed. Settlement of *H. banksii* under and outside canopies in the *Cystophora* zone did not show a clear pattern of canopy effect, with settlement not significantly different under and outside canopies ($F_{1,194}$=0.77, p=0.38) (Fig. 2.3).

**Table 2.3.** ANOVA results of *Hormosira banksii* settlement across years, seasons, months, weeks and zones. Cochran's test was significant, but log transformed data gave a better approximation of normal data on line plots. *n* = 3.

| Source of variation | Effect | SS | df | MS | *F* | p |
|---|---|---|---|---|---|---|
| Year | Fixed | 7.3437 | 2 | 3.67 | 1.51 | 0.234 |
| Season (Year) | Fixed | 58.5259 | 9 | 6.50 | 2.68 | **0.017** |
| Month (Season, Year) | Fixed | 142.5723 | 24 | 5.94 | 2.45 | **0.007** |
| Week (Month, Season, Year) | Random | 87.2954 | 36 | 2.42 | 9.07 | **0.000** |
| Zone | Fixed | 8.5495 | 3 | 2.85 | 10.66 | **0.000** |
| Year x Zone | Fixed | 0.8330 | 6 | 0.14 | 0.52 | 0.792 |
| Season (Year) x Zone | Fixed | 15.2725 | 27 | 0.57 | 2.12 | **0.004** |
| Month (Season, Year) x Zone | Fixed | 24.7105 | 72 | 0.34 | 1.28 | 0.119 |
| Week (Month, Season, Year) x Zone | Random | 28.8595 | 108 | 0.27 | 5.55 | **0.000** |
| Error | | 27.7113 | 576 | 0.05 | | |

**Table 2.4.** ANOVA results of *Hormosira banksii* settlement between weeks, zones and habitats in the Mid and Low *Hormosira* zones. Cochran's test was significant and variances could not be stabilized so raw averages were used. *n* = 3.

| Source of variation | Effect | SS | df | MS | *F* | p |
|---|---|---|---|---|---|---|
| Week | Random | 17105456 | 65 | 263161 | 3.39 | **0.000** |
| Zone | Fixed | 195188 | 1 | 195188 | 7.92 | **0.006** |
| Habitat | Fixed | 1380147 | 2 | 690073 | 10.42 | **0.000** |
| Week x Zone | Random | 1602650 | 65 | 24656 | 1.87 | **0.001** |
| Week x Habitat | Random | 8616079 | 130 | 66278 | 5.01 | **0.000** |
| Zone x Habitat | Fixed | 211031 | 2 | 105516 | 7.98 | **0.001** |
| Week x Zone x Habitat | Random | 1718498 | 130 | 13219 | 1.00 | 0.472 |
| Error | | 10312355 | 784 | 13154 | | |

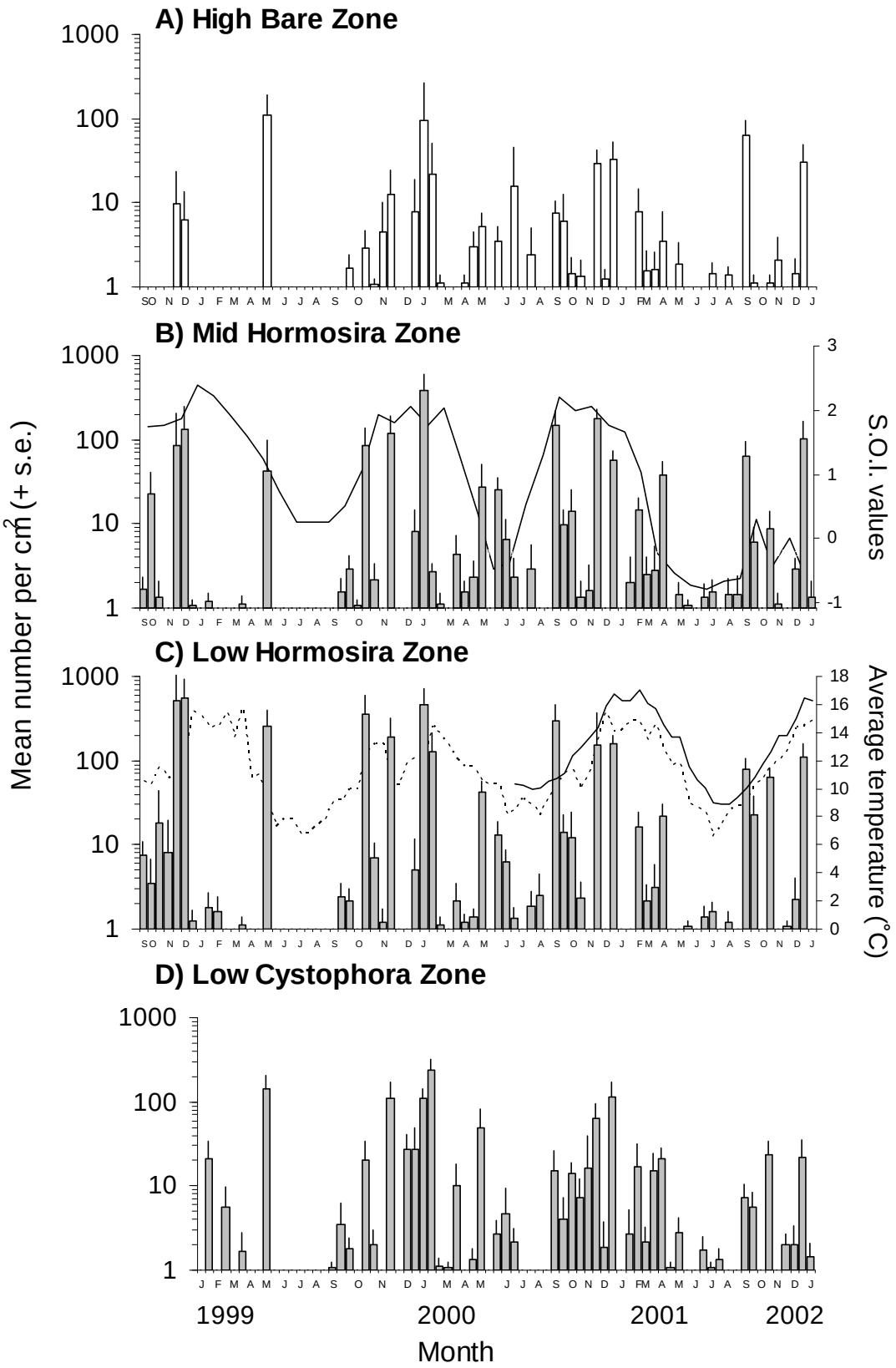


**Figure 2.2.** *Hormosira banksii*. Weekly settlement in the High Bare zone (A), Mid *H. banksii* zone (B), Low *H. banksii* zone (C), and Low *Cystophora* zone (D). Data are from the '-canopy' habitats for the mid and low zones, and the 'bare' habitat for the high zone. Refer to methods for detailed descriptions of each zone. Replicates = 3. 3 month running average SOI values are shown in 'B' (solid line). Average fortnightly air temperature (dashed line) and sea surface temperature (solid line) are shown in 'C'.

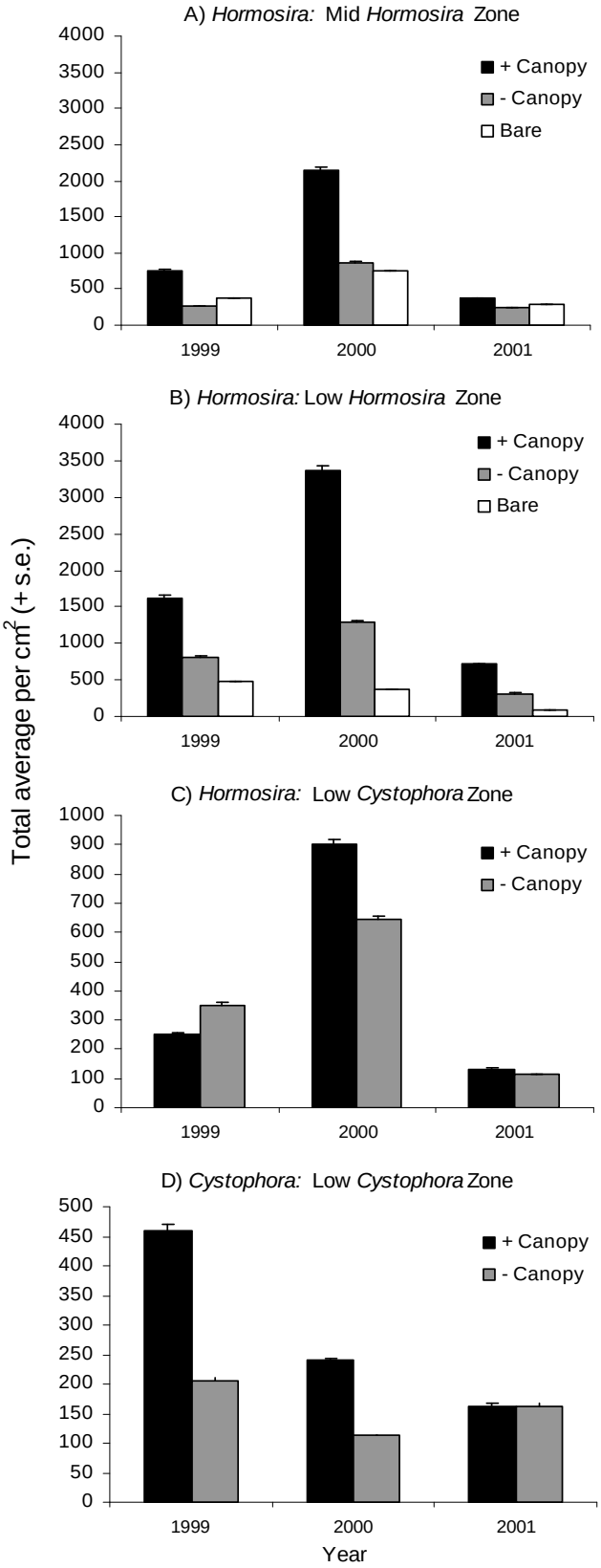


**Figure 2.3.** *Hormosira banksii* settlement in each habitat in the Mid *H. banksii* zone (A), Low *H. banksii* zone (B), and Low *Cystophora* zone (C). *Cystophora* spp. settlement in each habitat in the Low *Cystophora* zone (D). Data are cumulative annual totals.

***Cystophora* spp.**

Patterns of settlement for *Cystophora* spp. showed an annual cycle similar to that of *H. banksii*. Settlement occurred throughout the year but was greatest in spring and summer (Fig. 2.4, Table 2.5.), with a maximum average settlement of 301 (s.e.213) $cm^{-2}$ in the LCZ in December 1999. Settlement varied considerably between zones (Table 2.5.). The greatest settlement densities occurred in the LCZ, with little or no settlement in the higher zones. In this zone, settlement was greatest during the summer of 1999, but in 2001 settlement was greatest in spring. There was significant variation in the settlement of *Cystophora* spp. within each month, and between seasons (Table 2.5.). There was no correlation between monthly average settlement and monthly average air temperature or SOI values. *Cystophora* spp. settlement was correlated with *H. banksii* settlement ($r_{75}$=0.271, p=0.0192), with *Cystophora* settlement occurring 69% of the monitor periods that *H. banksii* settlement occurred. However, *Cystophora* spp. settlement densities were considerably lower. *Cystophora* spp. did not have significantly different densities settling under and outside canopies in the LCZ in the weekly periods ($F_{1,195}$=3.04, p=0.09), but cumulative annual totals show that settlement under the canopy was more than double than outside the canopy in 1999 and 2000 (Fig. 2.3, D).

**Table 2.5.** ANOVA results of *Cystophora* spp. settlement across years, seasons, months, weeks and zones. Cochran's test was significant, but log transformed data stabilized the variances.

| Source of variation | Effect | SS | df | MS | *F* | p |
|---|---|---|---|---|---|---|
| Year | Fixed | 0.410 | 2 | 0.205 | 1.176 | 0.320 |
| Season (Year) | Fixed | 5.762 | 9 | 0.640 | 3.670 | **0.002** |
| Month (Season, Year) | Fixed | 6.967 | 24 | 0.290 | 1.665 | 0.081 |
| Week (Month, Season, Year) | Random | 6.279 | 36 | 0.174 | 1.892 | **0.006** |
| Zone | Fixed | 21.489 | 3 | 7.163 | 77.695 | **0.000** |
| Year x Zone | Fixed | 1.530 | 6 | 0.255 | 2.767 | **0.015** |
| Season (Year) x Zone | Fixed | 13.594 | 27 | 0.503 | 5.461 | **0.000** |
| Month (Season, Year) x Zone | Fixed | 16.442 | 72 | 0.228 | 2.477 | **0.000** |
| Week (Month, Season, Year) x Zone | Random | 9.957 | 108 | 0.092 | 6.853 | **0.000** |
| Error | | 7.749 | 576 | 0.013 | | |

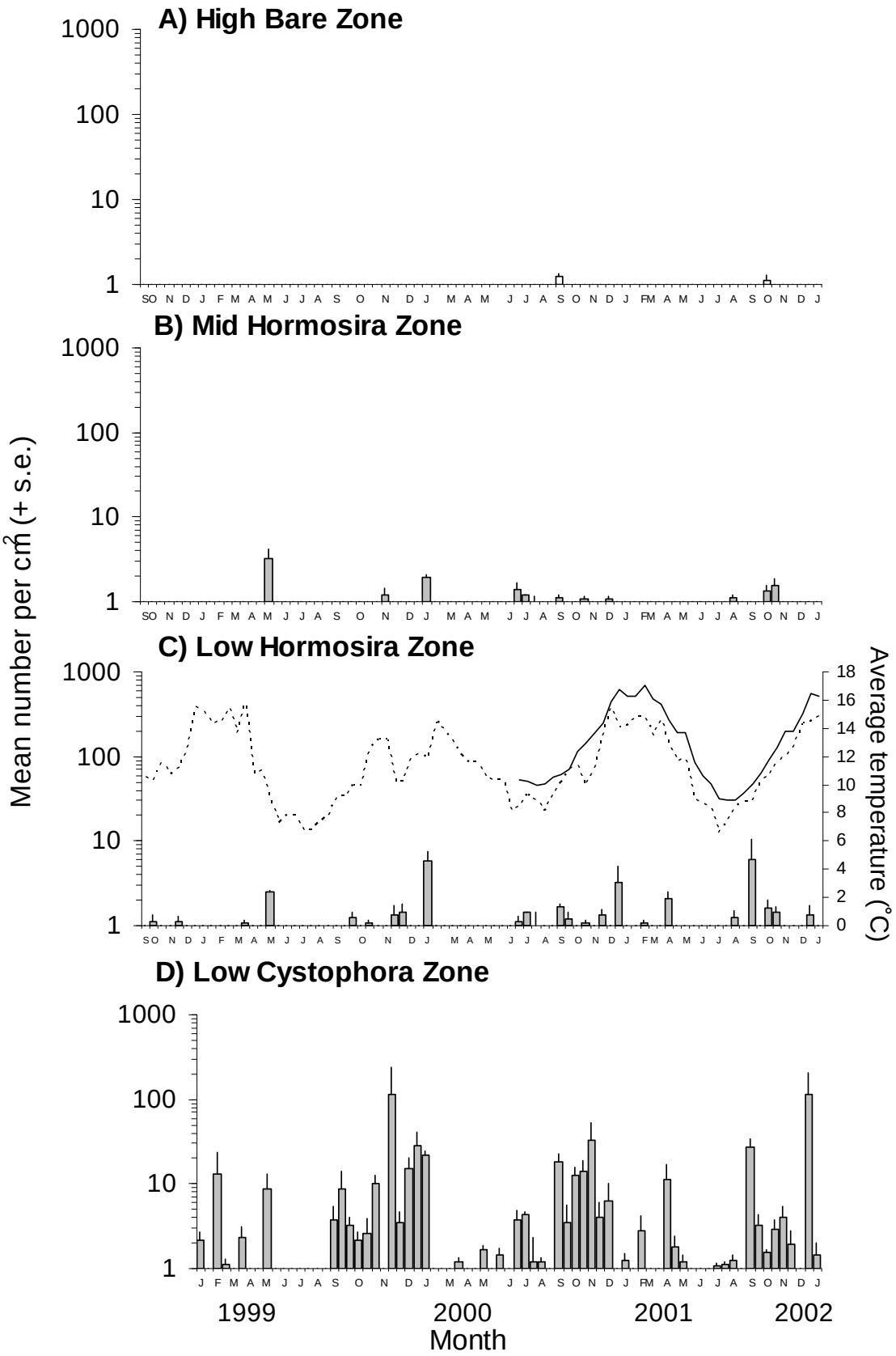


**Figure 2.4.** *Cystophora* spp. Annual settlement in the High Bare zone (A), Mid *H. banksii* zone (B), Low *H. banksii* zone (C), and Low *Cystophora* zone (D). Data are from the '-canopy' habitats for the mid and low zones, and the 'bare' habitat for the high zone. Refer to methods for detailed descriptions of each zone. Replicates = 3. Average fortnightly air temperature (dashed line) and sea surface temperature (solid line) are shown in 'C'.

### 2.3.2. Daily vs. weekly settlement patterns

In general, daily patterns of settlement in the different habitats were similar to weekly patterns, with non-significant duration x habitat interaction effects for April, May and November (Table 2.5). Greatest settlement usually occurred under the canopy (Fig. 2.5). Unadjusted settlement on the plates left in the field for one day was greater than on plates left in the field for one week, but during September 2002, the opposite was true (Fig. 2.5). During this sampling interval, *Cystophora* spp. settlement was also recorded on the weekly plates, but not on the daily plates (Dunmore, unpublished data). Plates placed in the mid shore in April and May 2000 also showed similar patterns of settlement between daily and weekly plates (Dunmore, unpublished data).

**Table 2.6.** Summary of ANOVA tests (Mean square and *F* values) of daily and weekly (Duration) *Hormosira banksii* settlement in the different habitats (+ canopy, - canopy, bare) in April and May 2000 and September and November 2002. Cochran's tests were significant, but log transformed data had more conservative p-values. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

| Source of variation | *df* | April | | May | | September | | November | |
|---|---|---|---|---|---|---|---|---|---|
| | | MS | *F* | MS | *F* | MS | *F* | MS | *F* |
| Duration | 1 | 0.32 | 3.53 | 0.23 | 3.21 | 12.89 | 166.02*** | 2.72 | 30.64*** |
| Habitat | 2 | 0.24 | 2.71 | 0.66 | 9.15** | 1.00 | 12.83** | 0.03 | 0.38 |
| Duration x habitat | 2 | 0.13 | 1.47 | 0.05 | 0.70 | 0.43 | 5.55* | 0.08 | 0.96 |
| Error | 12 | 0.09 | | 0.07 | | 0.08 | | 0.09 | |

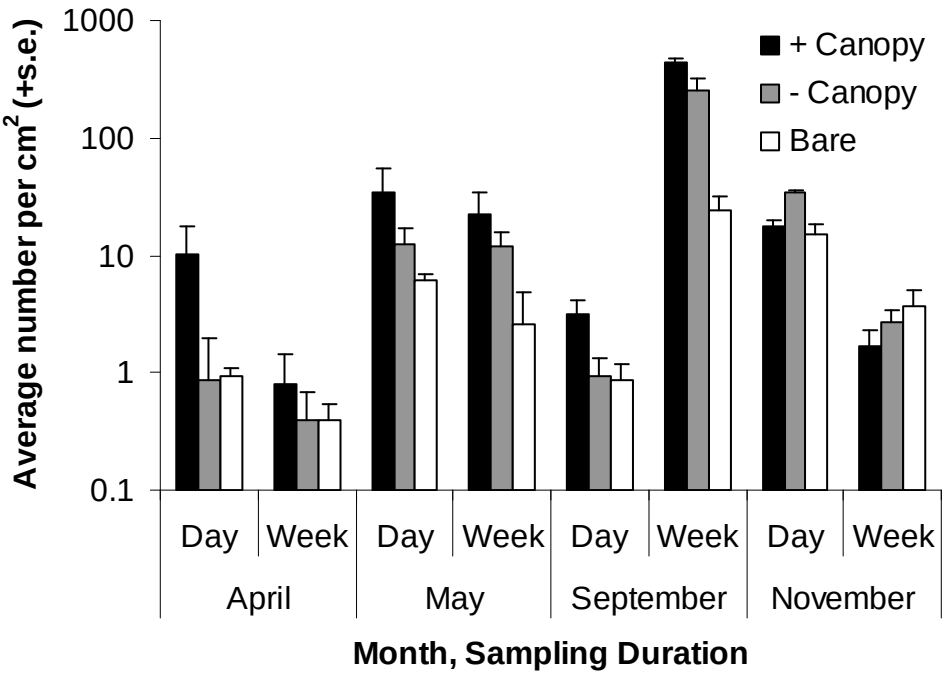


**Figure 2.5.** *Hormosira banksii.* Daily vs. weekly settlement in different habitats in the low *Hormosira* zone. Replicates = 3.

### 2.3.3. *Hormosira banksii* settlement between sites

Settlement during October 2001 – February 2002 in Mudstone Bay and Raramai were positively correlated, but no other sites were significantly correlated (Fig. 2.6, Table 2.7). Raramai, one of the smallest populations of *H. banksii*, had the highest settlement observed over the duration of the experiment, with an average of 396 (s.e. 115) propagules settling per $cm^2$ in October 2001 (Fig. 2.6).

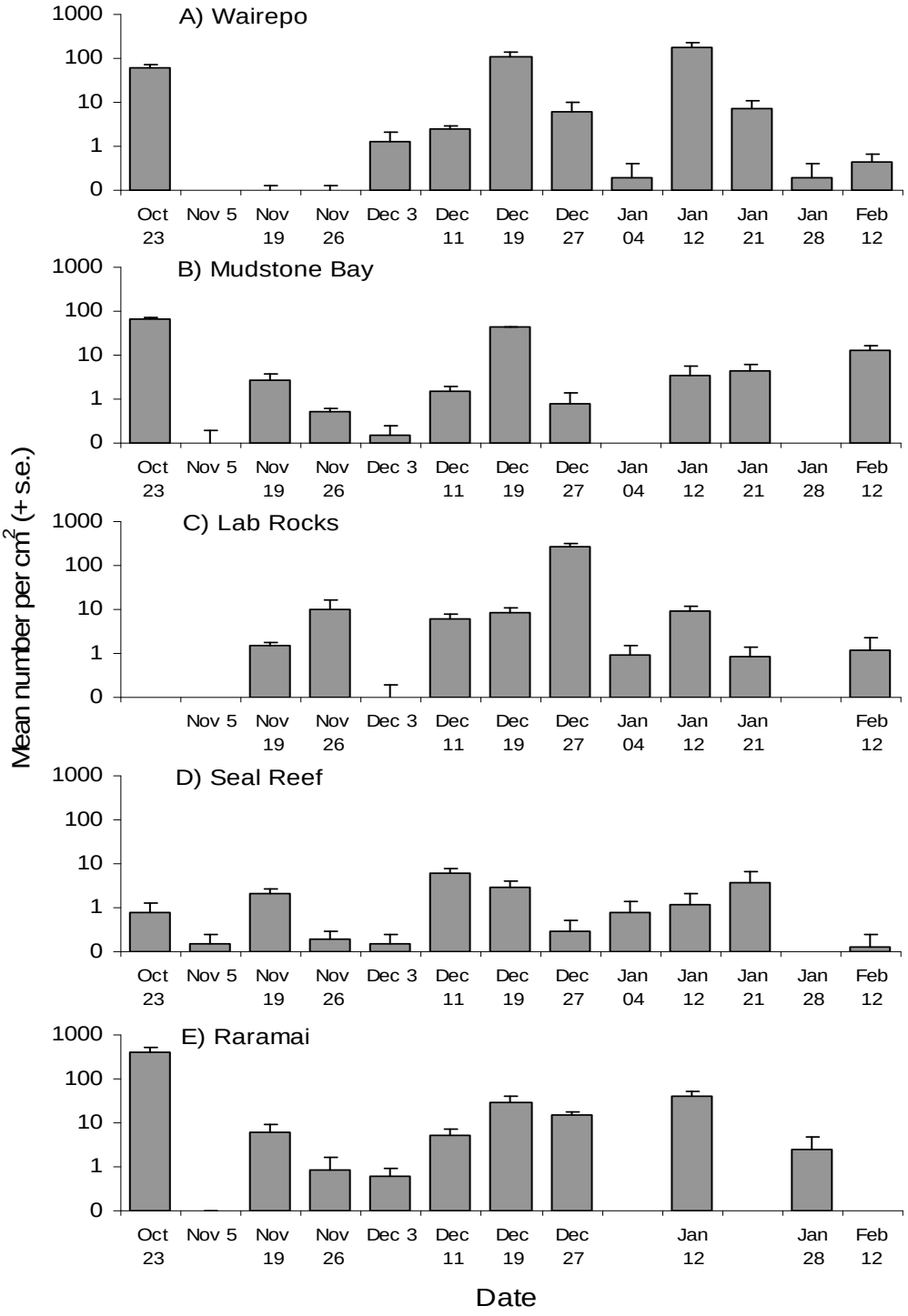


**Figure 2.6.** *Hormosira banksii* weekly settlement from October 2001 – February 2002 at Wairepo (A), Mudstone Bay (B), Lab Rocks (C), Seal Reef (D), and Raramai (E). Replicates = 3. Non-labelled dates indicate missing data.

**Table 2.7.** Correlation matrix for average *Hormosira banksii* settlement at each site. ($r_{11}$= 0.801; p<0.001***)($r_{13}$ = 0.760; p<0.001)

| | Wairepo | Mudstone Bay | Lab Rocks | Seal Reef |
|---|---|---|---|---|
| Mudstone Bay | 0.44 | | | |
| Lab Rocks | -0.09 | -0.13 | | |
| Seal Reef | 0.10 | 0.07 | -0.22 | |
| Raramai | 0.28 | 0.83*** | 0.14 | -0.06 |

## 2.4. Discussion

*Hormosira banksii* and *Cystophora* spp. settlement occurs year-round, but peaks and troughs are highly seasonal. Peak settlement occurred in spring and early summer, with quiescent phases during winter. Settlement is indicative of reproductive activity, and year-round reproduction is in contrast to many other species of temperate algae which usually have more restricted reproductive seasons (Hoffmann 1987). For example, North Atlantic fucoid species have asynchronous seasonal reproductive periodicity. *Ascophyllum nodosum* is reproductive in late spring and early summer, *Fucus spiralis* is active in summer, *Fucus vesiculosus* is mainly reproductive in the autumn and winter, and *Fucus distichus* reproduces mainly during winter (Brawley and Johnson 1992). This partitioning of reproductive periodicity results in a more uniform supply of propagules of different species throughout the year (Santelices 1990).

The synchronous reproduction of *H. banksii* and *Cystophora* spp. has potentially important ecological consequences for competitive interactions. Year-round reproduction may enable *H. banksii* and *Cystophora* spp. to maximize their reproductive success by taking advantage of small 'windows of opportunity', i.e. short periods when favourable environmental and biological conditions coincide and allow successful settlement and subsequent recruitment (Deysher and Dean 1986, Reed et al. 1988). However, there is a trade-off for reproducing throughout the year. Propagules settling in spring and early summer are exposed to warmer conditions and increased light that may enhance growth rates, but these same conditions may cause higher mortality due to harsher environmental conditions such as heat stress and desiccation. In contrast, propagules settling in cooler months may experience a more benign thermal environment with less desiccation stress. However, wave climates are generally harsher in winter which can make attachment difficult (Taylor 2002, Taylor and Schiel 2003), and slower growth due to cooler temperatures and reduced light will result in settlers being exposed to size-dependent grazing for much longer (Vadas et al. 1992).

Synchronous reproduction may also increase the chances of hybridization of closely related species (Santelices 2002). This may be particularly relevant for *Cystophora* species which are often found in close proximity. This study examined settlement over week long periods, but gamete release may be asynchronous between species on a much smaller scale.

For example, closely related species have been shown to release gametes at different times during the same morning (Clifton 1997, Clifton and Clifton 1999). If fertilization occurs fairly rapidly, this reduces the potential for hybridization.

Settlement of *H. banksii* was correlated with the southern oscillation index (SOI). The SOI gives a general indication of the state of the sea; sustained positive values occur in La Niña years when sea surface temperatures are warmer, and wind and waves tend to be calmer. Sustained negative values occur in El Niño events, when sea surface temperatures are cooler, and wave action is generally stronger. A correlation with the SOI is an indication that settlement may be influenced by broad-scale, long-term environmental conditions. However, this does not preclude that fine scale, short-term conditions fluctuating on a daily basis are also important.

Settlement of *H. banksii* was synchronous across zones, but the density of settlement varied greatly. This may be a result of differences in size and density of adult plants in each zone, coupled with low dispersal. *H. banksii* has conceptacles on the whole plant and, therefore, larger plants in more dense stands of *H. banksii* in the LHZ have the potential to produce more gametes, leading to higher settlement densities. *Cystophora* settlement was also synchronous across zones, but settlement densities were much lower in higher zones. This was not surprising given that the main source of *Cystophora* spp. settlers for all zones was plants in the LCZ since few mature plants were observed higher on the shore.

Synchronous settlement within sites does not necessarily translate to synchronous settlement between sites**.** We found that sites separated by only one kilometre could be asynchronous in both the occurrence and magnitude of settlement. This may be due to differences in local-scale environmental cues for gamete maturation and release. For example, settlement often occurs in warm, calm conditions which may not be experienced at some sites due to differences in wind and wave exposure. Raramai, Mudstone Bay and Seal Reef are subjected to south and southeast winds and swells, while Lab Rocks and Wairepo are exposed to north and northeast conditions.

Sites with larger stands of algae did not necessarily have higher settlement. One of the smallest populations (Raramai) produced settlement in one week that was the highest for all sites over the entire experiment. Settlement at each site was measured within low-shore patches of *H. banksii*, and dilution and diffusion may have a stronger influence on density of settlement with increasing distance from the population. Thus the site with the largest *H. banksii* population (Wairepo) may have a larger dispersal shadow than the smaller sites.

Settlement or reproduction can also vary on a much larger geographical scale. Begum (1980) examined *H. banksii* plants from a site in the north of the North Island of New Zealand

and found greatest liberation of gametes in July-October (winter - spring). In contrast, in the present study peak reproduction (measured as settlement) occurred later in the year, from October-January (spring – early summer). Temperature can impose boundaries on species by limiting reproduction, growth or survival (van den Hoek 1982). Some species at the limits of their distributional ranges reproduce less often and produce fewer gametes. This can affect their dispersal potential, settlement rates and abilities to recover from disturbance (Anderson and North 1966, Hoffmann 1987, Norton 1992, Reed et al. 1997, Reed et al. 2004). At warmer latitudes it would be expected that *H. banksii* and *Cystophora* spp. populations would have peak reproduction earlier, reproduce less often and perhaps be less fecund.

Most algal species reproduce prolifically and consequently some propagules survive massive mortality during the early life stages to successfully recruit (Chapman 1984, Santelices 1990, Cervin et al. 2004, Dudgeon and Petraitis 2005). Vadas et al. (1992) likened the intense production of spores to mast years of terrestrial plants. By swamping areas with propagules during optimal environmental conditions, germlings have a higher chance of escaping predation, but can be subjected to intense intraspecific competitive interactions that can affect growth and survival (Black 1974, Lubchenco 1983, Reed 1990b, Reed et al. 1991). Positive effects of density on growth and survival have also been reported (Schiel and Choat 1980, Schiel 1985, Ang(jr) and DeWreede 1992). Schiel and Choat (1980) and Schiel (1985) found faster growth of subtidal plants in high density stands. This was possibly a result of a reduction in water flow in high density areas which decreased physical battering. Ang (jr) and DeWreed (1992) suggested that tuft-forming high densities of intertidal *Fucus* germlings may have an advantage against desiccation and herbivory. Clearly, there are both positive and negative consequences of synchronous reproduction and high settlement densities.

Reed (1990a) found a minimum settlement density of at least 1 spore/mm$^2$ was required for successful recruitment in *Macrocystis pyrifera* and *Pterygophora californica*. This settlement density was defined by the maximum distance that can separate male and female gametophytes while ensuring successful fertilization. Unlike these two species, fucoids have no alternation of generations, and therefore do not have the same requirements of settlement density for fertilization. However, a minimum density of settlement may be required to produce and maintain a viable population of plants. Schiel (2004) determined that *H. banksii* requires >1 recruit cm$^{-2}$ to produce a closed canopy, and equated that to approximately 250 – 750 settlers cm$^{-2}$. In our study, 250 – 750 settlers per cm$^2$ occurred several times during three years in the LHZ, but only occurred once in the MHZ and LCZ. Densities of this magnitude were never detected in the HBZ. Frequent reproductive periodicity would enhance settlement by supplementing densities, but post-settlement interactions with the physical and biological

environment (e.g. heat stress and desiccation in the High and Mid zones, and competition with *Cystophora* spp. in the low zone) may prevent or slow recruitment in these areas. For example, recovery of *H. banksii* in cleared plots in the mid shore at the same site was at least 5 years slower than in plots in the low shore (Schiel 2006).

Settlement of *H. banksii* was greater under the canopy in the MHZ and LHZ, but not in the LCZ. The increased settlement under an adult canopy supports the suggestion that *H. banksii* has restricted dispersal, with most propagules falling beneath adult plants. *H. banksii* gametes are often released at low tide, and remain on the outside of conceptacles until the incoming tide washes them off of the plants. Eggs are 65-75 μm in diameter and are negatively buoyant (Forbes and Hallam 1978). This, coupled with the fact that fucoid algae release gametes during periods of calm oceanic conditions (Serrao et al. 1996, Pearson et al. 1998), suggests *H. banksii* eggs have little chance of traveling great distances. Furthermore, this localised dispersal may be influenced not only by propagule characteristics, but also by altered hydrodynamic conditions due to the presence of the adult plants, thereby producing a deposition sink (Santelices 1990, Brawley 1992).

In contrast to *H. banksii*, the greatest settlement densities of *Cystophora* spp. did not occur under an adult canopy. This could be a result of the larger adult *Cystophora* plants releasing eggs with potentially longer trajectories that disperse beyond the bounds of the source canopy. Negatively buoyant eggs released higher in the water column will disperse further because they take a longer time to reach the substratum (Santelices 1990, Norton 1992). However, the lack of *Cystophora* spp. settlement outside the LCZ indicates that these algae also have relatively localised dispersal. *Cystophora* eggs are larger (~100 μm in diameter) than *H. banksii* eggs and sink twice as fast (refer to Chapter 3). The potentially longer trajectory of eggs released high in the water column by large adult *Cystophora* plants may therefore be counteracted by the faster sinking rates of their large eggs.

Despite their localised dispersal, *H. banksii* and *Cystophora* spp. still have the potential for long range dispersal through the detachment and drifting of adult plants, and the release of gametes at a distant site. This method of dispersal may be particularly effective for *Cystophora* spp. because the plants are monoecious, allowing for self-fertilisation. *H. banksii* is dioecious and would require male and female plants to arrive together at a site for fertilisation to occur. However, *H. banksii* is very susceptible to disturbance events such as storms (Underwood 1998, Underwood 1999) or pedestrian traffic (Schiel and Taylor 1999), and the loss of many plants at one time would enhance numbers arriving at a distant site and hence the chances of successful fertilisation. Most drift plants end up as beach cast, high on the shore. Beach cast *H. banksii* have been observed releasing gametes (Dunmore, pers. obs.),

but it is not known whether these are able to complete successful fertilisation and then disperse to suitable habitats lower on the shore. However, drifting plants collected over *H. banksii* habitats have been observed releasing gametes (Dunmore, pers. obs.) and it seems likely that this may be an effective method for settlement in a suitable habitat. This mode of dispersal may be important in gene flow between populations and the colonisation of new areas.

Daily and weekly patterns of settlement confirmed that settlement of *H. banksii* was usually greater under an adult canopy, and that the patterns observed on the weekly plates were not a result of differential post-settlement mortality between habitats. On some occasions post-settlement mortality did reduce overall densities, but the patterns were similar between habitats. This gave us confidence in the duration for which plates were left in the field; leaving the plates for shorter periods may have reduced post-settlement mortality, but we may have missed settlement. For example, in September 2002 *Cystophora* spp. settlement was observed on the weekly plates but not on the daily plates.

Many studies have shown disparity between settlement and recruitment patterns, with little or no recruitment occurring in areas that receive high densities of settlers (such as under an adult canopy) (Dayton et al. 1984, Brawley and Johnson 1991, Kendrick and Walker 1995, Bellgrove et al. 1997, Johnson and Brawley 1998). This disparity was evident in *H. banksii* and *Cystophora* communities in this study. We found very high settlement densities of *H. banksii* (c. 3300 settlers $cm^{-2}$ $year^{-1)}$ and *Cystophora* spp. (c. 460 settlers $cm^{-2}$ $year^{-1}$) under adult canopies where little or no recruitment occurs (Dunmore, unpublished data). Furthermore, this is likely to be an underestimate of settlement because plates were not in the field all of the time. This appears to be a significant waste of supply, but many propagules are required to ensure survival due to high mortality at early life stages, and this may be an important means of taking advantage of stochastic disturbances that open patches in canopies.

Patchiness in *H. banksii* canopies is common because plants have small holdfasts and are easily dislodged, opening small gaps that provide space for recruitment. Experimental removals of *H. banksii* and *Cystophora* spp. canopies have produced intense recruitment (Schiel and Taylor 1999, Lilley and Schiel 2006, Schiel 2006). Although successful recruitment under a canopy is restricted by many biological and physical variables (Vadas et al. 1992), propagules that do settle under a canopy have been compared to a terrestrial 'seed bank' (Santelices 1990, Ang(jr) 1991, Hoffmann and Santelices 1991, Ang(jr) and DeWreede 1992, Creed et al. 1996), producing recruits if the canopy is removed by a disturbance event. However, the time frame of a marine compared with a terrestrial 'seed bank' is very different. While in terrestrial systems seeds may lay dormant for several years, marine banks of

propagules are not dormant but have slow or suspended growth (especially during cooler months) which can result in them remaining microscopic for several months. This strategy of surviving unfavourable conditions, combined with year-round reproduction, may enable *H. banksii* and *Cystophora* spp. to dominate successional processes.

This chapter illustrates the major variation in settlement that occurs on very small spatial and temporal scales. The lack of recruitment into bare rock patches by *H. banksii* does not appear to be driven by a lack of propagule supply. This local scale variation in recruitment is probably driven by early post-settlement mortality. However, dispersal does appear to be fairly limited, with a disproportionate number of *H. banksii* propagules settling beneath adult plants and reduced *Cystophora* spp. settlement above the *Cystophora* zone. The following chapters examine dispersal capabilities more in more detail, and investigate post-settlement interactions of propagules with the physical and biological environment.

# Chapter 3
# Local-scale dispersal

## 3.1 Introduction

Dispersal is one of the most fundamental, yet least understood, processes in population dynamics (Gadgil 1971, Nathan & Muller-Landau 2000). Information on dispersal is essential for understanding species distributions and abundances, range expansion and invasions, the genetic structure, recovery and replenishment of populations, and ecological interactions. Much of our current knowledge of dispersal is biased towards terrestrial systems and marine invertebrates (Gaines & Bertness 1993), and information on marine algae is generally sparse (Santelices 1990, Schiel 2004, Schiel & Foster 2006). Marine invertebrates have an obligate planktonic period and are motile; consequently transport can be extensive (1000's of kilometers). In contrast, most marine algae do not have a planktonic stage and have non-motile, negatively buoyant propagules; subsequently dispersal is far more restricted (Kinlan & Gaines 2003, Kinlan et al. 2005). Despite their limited dispersal in comparison to invertebrates, algal dispersal estimates are very broad, ranging from only a few meters to tens of kilometers (Norton 1992) and are highly dependent on the taxa involved.

In general, early successional, opportunistic algae have relatively long distance dispersal, and most late successional, perennial algae have poor dispersal (Amsler & Searles 1980, Hoffmann & Ugarte 1985). However, there is evidence that that some perennial algae also have the potential for relatively long distance dispersal (Reed et al. 1988, Fredriksen et al. 1995, Gaylord et al. 2002). For example, the kelp *Pterygophora californica* can disperse at least 4000 m (Reed et al. 1988), whilst *Laminaria hyperborea* disperses at least 200 m (Fredriksen et al. 1995). One problem with dispersal estimates is that many studies have focused on recruitment with increasing distance from populations (Anderson & North 1966, Dayton 1973, Hruby & Norton 1979, Deysher & Norton 1982, Vandermeulen & DeWreede 1986, Arrontes 2002), and have not considered the considerable mortality that occurs after settlement. This can result in an underestimation of dispersal because propagules may actually disperse further, but recruitment may often only be successful close to adult populations. Dispersal away from a population can take propagules outside physiologically favourable habitats, and/or biological pressures can increase with increasing distance from source populations. This is particularly significant on intertidal shores, where physical and biological conditions change greatly over a scale of meters or less.

Dispersal distances are highly variable according to species characteristics and habitat features. Dispersal is a function of propagule characteristics and behaviour, height of gamete release above the substratum, the density of adult plants, substrate type, topography and hydrodynamic conditions (see reviews by Santelices 1990, Norton 1992). Propagule characteristics and behaviour influence sinking rates, and in conjunction with height of release

above the substratum, affect the amount of time in the water column. Many studies have examined how propagule shape, size and density, and the presence of a mucilage sheath affect sinking velocity. In general, smaller eggs sink more slowly than larger eggs (Coon et al. 1972, Okuda & Neushul 1981, Hoffmann & Camus 1989), and a mucilage sheath around the spore or egg can increase the total volume and slow sinking rates (Boney 1975, 1978). Boney (1975) found that the mucilage sheath contributed 53-88% of the total spore and mucilage volumes in 14 species of red algae. It was hypothesized that the mucilage enhanced spore buoyancy and assisted dispersal. Mucilaginous exudate also affects dispersal. Spores of red algae are often released in a viscous mucilage which floats on the water surface, and the spores descend from the mucilage over larger areas (Boney 1978). In contrast, some algae (e.g. *Fucus* spp., *Postelsia palmaeformis*) release gametes or spores with copious amounts of viscous mucus during low tide. The mucus carries the gametes or spores to the substrate during low tide and reduces dispersal (Paine 1979, Brawley & Johnson 1992, Brawley et al. 1999).

The height above the substratum at which gametes or spores are released can have a large effect on dispersal, but this is not always related to plant size (Norton 1992). *Macrocystis pyrifera* is a large kelp, reaching lengths of up to 60 meters, but reproductive structures are located at its base which reduces the amount of time spores are in the water column. In contrast, *Laminaria hyperborea* is much smaller but has sori located on the entire lamina, and can release spores from heights of 3m above the benthos (Fredriksen et al. 1995). Spores released higher in the water column drift for longer periods and are carried further.

The hydrodynamic environment that propagules encounter has a great influence on dispersal (Norton 1992). The environment is modified by large-scale factors such as currents and wave action, and fine-scale factors such as surface micro-topography which can modify flow in the boundary layer. Dispersal of the kelps *M. pyrifera* and *P. californica*, and the filamentous brown alga *Ectocarpus siliculosus* is greatly increased during winter storms by the action of turbulent mixing re-suspending spores and transporting them considerable distances (Reed et al. 1988). However, some fucoid algae have been shown to release gametes in periods of calm hydrodynamic conditions, which limits their dispersal (Pearson & Brawley 1996, Serrao et al. 1996, Pearson & Brawley 1998, Pearson et al. 1998).

The presence of other plants alters hydrodynamic conditions by reducing flows and altering turbulence (Norton 1992, Hurd & Stevens 1997, Hurd 2000, Ackerman 2002, Gaylord et al. 2002). Reduced flows increase the chances of propagules settling, and turbulence can act to increase chances of deposition or re-suspension. Substrate and shore topography can have a large influence on dispersal by also affecting flow and turbulence.

*Sargassum muticum* propagules, settled in the laboratory under flowing water, accumulated in depressions rather than on peaks of the micro-topography, and smooth substrates were unfavourable for settlement (Norton & Fetter 1981).

Distributions and abundances of algae are generally thought to be set by physical and biological stresses acting on early post-settlement and recruit stages. Few studies have examined the supply of propagules to an area, its variability over small temporal and spatial scales and how this relates to recruitment. Distributions and abundances may be highly constrained by limited dispersal capabilities. Propagules may simply not reach areas (Underwood & Denley 1984, Underwood 1991), or reduced settlement densities with distance from a source may result in higher mortality and subsequently low recruitment. High settlement densities are particularly important for species that have an alternation of generations that require microscopic male and female gametophytes to be in close proximity for successful fertilisation to occur. Reed (1990) found that at least 1 spore/mm$^2$ was required for successful fertilisation and subsequent recruitment of sporophytes of *M. pyrifera* and *P. californica*. Dayton (1973) postulated that the concentration of young sporophytes of *P. palmaeformis* around the holdfasts of adults was due to a dependency of recruitment upon a saturation of spores. The positive effect of density on survival of intertidal species is usually a result of a reduction in desiccation and grazing. Hruby and Norton (1979) found higher initial densities increased survival of several species in a tidal simulator in laboratory experiments. Likewise, increased survival of high density *Fucus distichus* (= *Fucus gardneri*) germlings in field experiments in Canada has been linked to the tuft-like habit offering protection from desiccation and grazing (Ang & DeWreede 1992).

Fucoid algae are generally thought to have very low gamete dispersal capabilities, typically less than 30m (Sousa 1984, Kendrick & Walker 1991, Chapman 1995, van Tamelen et al. 1997, Johnson & Brawley 1998, Dudgeon et al. 2001). Their short dispersal is a result of several factors. Fucoid eggs and zygotes are relatively large (>30 $\mu$m), negatively buoyant, non-motile, and are released during periods of calm water (Serrao et al. 1996, Pearson et al. 1998). The short range dispersal of gametes and zygotes can be extended in many species by the detachment and dispersal of floating adults over long distances with subsequent release of gametes at a distant site. This has been considered instrumental in the geographical spread of *Sargassum muticum* (Fletcher 1980, Fletcher & Callow 1992). However, it is considered highly episodic and ineffective for most species of algae (van den Hoek 1987).

Information on dispersal and the densities at which species settle with increasing distance from populations is essential for predictions of range expansion, recovery from disturbance and gene flow between populations. This chapter determines egg sizes and

sinking rates of the New Zealand fucoids *Hormosira banksii*, *Durvillaea antarctica*, *Durvillaea willana* and *Cystophora torulosa*. It was hypothesized that larger eggs would sink faster. The dispersal of *H. banksii*, *Durvillaea* spp., *C. torulosa*, and the Oregon species *Fucus gardneri* was tested experimentally by examining settlement of germlings with increasing distance from a source. It was hypothesized that settlement would be highly localised, with greater settlement close to the source and an exponential decline in densities with increasing distance. It was expected that settlement would be very low at distances greater than 1 m.

## 3.2 Methods

### 3.2.1 Sites

Study sites in New Zealand were located on Kaikoura Peninsula, and approximately 12km south of the Peninsula (Fig. 3.1). The sites were Wairepo (42° 25' S, 173° 42' E), Seal Reef (42° 25' S, 173° 43' E), First Bay (42° 25' S, 173° 42' E), Mudstone Bay (42° 25' S, 173° 41' E), and Paratitahi (42° 26' S, 173° 34' E). Wairepo is a semi-sheltered mudstone platform that is dominated by *H. banksii* and *Cystophora* spp. in the mid and low shores respectively. This site was used for *H. banksii* and *C. torulosa* experiments. First Bay and Mudstone Bay, semi-sheltered mudstone platforms with an abundance of *H. banksii*, were also used for a *H. banksii* experiment. *D. antarctica* experiments were at Seal Reef and Paratitahi, exposed sites that were dominated by *D. antarctica* in the low shore. The experiment in Oregon on *F. gardneri* was at Fogarty Creek (44° 51' N, 124° 03' W) (Fig. 3.2) which is a semi-exposed basaltic platform with an abundance of *F. gardneri* in the high shore.

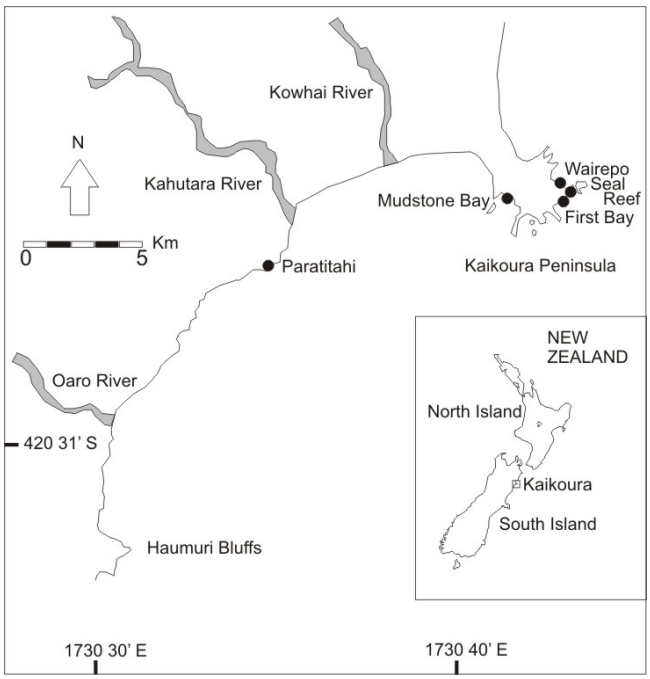


**Figure 3.1.** Map of Kaikoura Peninsula showing study sites and location within New Zealand.

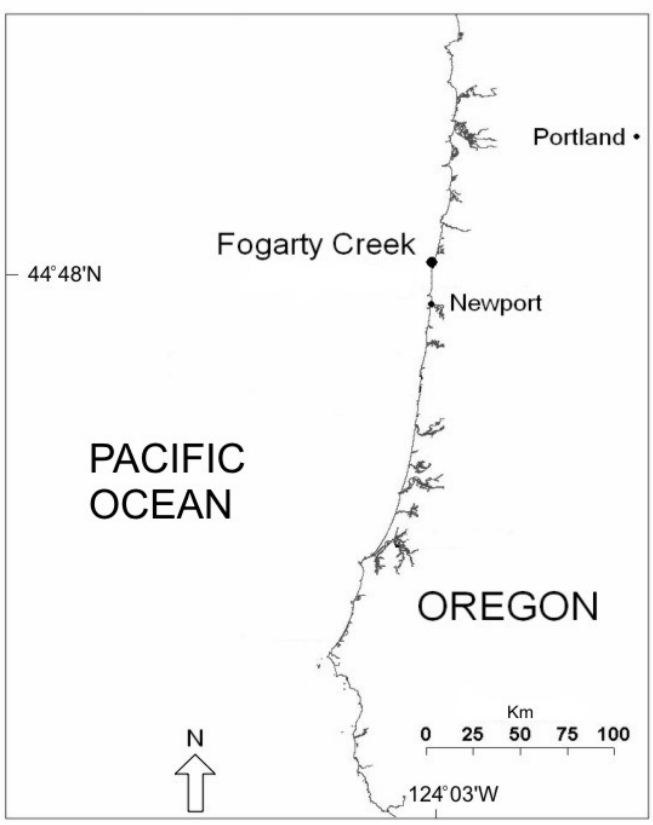


**Figure 3.2.** Map showing study site in Oregon, U.S.A..

### 3.2.2 Egg sizes and sinking rates

Eggs were obtained by collecting reproductive adult plants and cold-shocking them in a refrigerator for 1 to 3 d, and then placing them in a warm area for 1 to 2 h to stimulate gamete release. The sizes of 30 eggs of each species were measured using a compound microscope.

To obtain zygotes for estimation of sinking rates, gametes were washed from plants and left in buckets for approximately 30 min. for fertilisation to occur. The zygote suspension was passed through a 100 $\mu$m filter to remove debris. For two trials with *H. banksii*, unfertilised eggs were washed from female plants and used to determine sinking rates so that a comparison could be made with zygotes.

Sinking rates for *H. banksii*, *C. torulosa*, *D. antarctica* and *D. willana* were estimated by measuring the rate at which eggs or zygotes descended 1.5 mm through seawater. Filtered seawater was left in buckets for 24 h to acclimate close to room temperature, and then placed in a 1 L measuring cylinder and water bath. Room temperature was 13.5 ˚C and water temperature was 12.5 ˚C. The measuring cylinder was placed inside a water bath to reduce convection currents, and a dissecting microscope was positioned horizontally so that eggs could be viewed descending through the water in the measuring cylinder. Approximately 10ml of the zygote suspension was carefully introduced at the top of the measuring cylinder, and 15 random eggs or zygotes timed as they sank 1.5 mm. After this, the water was

discarded, clean water was introduced to the measuring cylinder, and the process was repeated. A total of 30 eggs or zygotes were measured per species.

### 3.2.3 Dispersal

#### General methods

Dispersal experiments tested the variation in density of propagule settlement with increasing distance from source populations. Settlement of propagules was measured using artificial plates attached to the rock substrate. Stainless steel mesh fences were used to exclude grazers (refer to chapter 2 for a description of plates and fences). Algal settlement was monitored using a dissecting microscope to count algal propagules in five haphazardly chosen 1cm$^2$ areas on each plate. To minimize possible edge effects, a 1 cm margin around the perimeter of each plate was excluded.

Plates were placed at increasing distances from source populations. Distances of plates from the nearest adult plant were measured from the farthest edge of the plate. The design of experiments was different according to the species studied because it was preferable to have a distinct algal margin from which plates could be arrayed. *Durvillaea* spp., *H. banksii*, and *F. gardneri* reproduce frequently, and the release of gametes is visually obvious at low tide. This made it easy to place plates on the shore when gamete release was evident, and collect them 24 h later. Gamete release of *Cystophora* spp. is not as obvious, thus a different method of measuring dispersal was trialled (refer to the *C. torulosa* section below).

#### *Durvillaea* spp.

Plates could be placed up the shore without the possibility of encountering other conspecific plants because *Durvillaea* spp. has a distinct low shore distribution margin. Germlings of *D. antarctica* and *D. willana* could not be distinguished from each other, and are therefore referred to as *Durvillaea* spp. Two sites were used; Paratitahi and Seal Reef. These were chosen because they had relatively flat platforms and plates could be arrayed up the shore with very little change in vertical height. Plates were placed on flat, horizontal surfaces. Paratitahi was used initially but the platform was not large enough because plates could be placed a maximum of only 8 m from *Durvillaea*. Seal Reef was used in subsequent experiments because plates could be placed up to 32 m from source plants. Seal Reef also had few *D. willana* plants, so settlement was likely to be *D. antarctica*. Seal Reef was also used in an experiment to test settlement of propagules on a vertical rock face, with increasing distance up to 1.10 m above a *D. antarctica* margin. Plates were placed on flat, vertical surfaces.

Each experiment had replicate arrays of plates (Table 3.1). At Paratitahi, replicates were approximately 10m apart, at Seal Reef replicates were approximately 15-20 m apart, and

for the vertical dispersal experiment at Seal Reef replicates were approximately 0.5 m apart. Experiments were repeated on several occasions (Table 3.1).

**Table 3.1** Designs of dispersal experiments.

| Species | Site | Distance farthest edge of plates from source (m) | Replicates | Repeated |
|---|---|---|---|---|
| *Durvillaea* spp. | Paratitahi | 0, 0.1, 0.35, 0.6, 1.1, 2.1, 4.1, 8.1 | 3 | 4x (May – Aug. 2001) |
| | Seal Reef | 0, 0.1, 0.35, 0.6, 1.1, 2.1, 4.1, 8.1, 16.1, 32.1 | 5 | 7x (Jul. - Aug. 2002) |
| | Seal Reef | 0, 0.1, 0.35, 0.60, 1.1 (on vertical rock face) | 2 | 3x (Jul. - Aug. 2002) |
| *H. banksii* | Wairepo, First Bay, Mudstone Bay, | 0, 0.1, 0.35, 0.60, 1.1, 2.1 | 3 | 1x (May 2001) |
| | Wairepo | 0, 0.1, 0.35, 0.60, 1.1, 2.1 | 3 | 4x (May, Oct. 2001; Jan., Nov. 2002) |
| *F. gardneri* | Fogarty Creek | 0, 0.1, 0.35, 0.60, 1.1, 2.1 | 3 | 2x (Jun. 2001) |
| *C. torulosa* | Wairepo | 0, 0.1, 0.35, 0.60, 1.1, 2.1 | 4 | 1x (Aug. 2000) |

***Hormosira banksii* and *Fucus gardneri***

*H. banksii* and *F. gardneri* can have patchy distributions, and it is difficult to find large areas that do not have isolated, or clumps of, conspecific plants. Sites were chosen that had distinct margins of algae. Plates were arrayed either within bare rock patches (for *H. banksii*) (Fig. 3.3) or within algal areas that had no conspecific plants (for *F. gardneri*) (Fig. 3.4). Plates were placed under an adult canopy, and 0.1, 0.35, 0.6, 1.1 and 2.1 m away from the adults ($n$=3) (Table 3.1). For *H. banksii*, experiments were done at Wairepo on 3 occasions, and once at different sites. *F. gardneri* experiments were done at Fogarty Creek (Table 3.1).

**Figure 3.3** A dispersal array of plates for *H. banksii* settlement at Wairepo, New Zealand. Algae surrounding bare rock patch are *H. banksii*.

**Figure 3.4** A dispersal array of plates for *F. gardneri* settlement at Fogarty Creek, Oregon. Algal patch in center is *F. gardneri*.

***Cystophora torulosa***

In August 2000, a single pilot experiment tested dispersal in *C. torulosa*. Reproductive adult plants were collected and cold shocked, then placed in a mesh bag and attached in the middle of a large, flat bare rock area, high on the shore. The nearest *Cystophora* plants were

approximately 20 m away. Plates were placed in four arrays in different directions (upshore, downshore, alongshore left, alongshore right), with increasing distance from the bag (0.1, 0.35, 0.6, 0.85, 1.1, 1.6 and 2.1 m) (Table 3.1). Settlement numbers on whole plates were counted because only a few adult plants were used and settlement densities were low. Data were converted to numbers per $cm^2$ for comparison with other experiments. Due to lack of replication of plates in each direction and through time, data were merged and direction of array was not analysed separately.

### 3.2.4 Analyses

Cochran's test was used to test homogeneity of variances, and data were log-transformed if necessary. General linear model ANOVAs were used to test the variation in sinking rates between species, and the variation in settlement densities over distance from populations. In both cases, time was treated as random. Exponential or linear regression lines were fitted to the data. Data were displayed graphically as continuous variables so that the nature of the numbers against distance was evident. When settlement numbers were variable, a log scale was used to highlight differences.

## 3.3 Results

### 3.3.1 Egg sizes and sinking rates

*C. torulosa* had the largest eggs at approximately 100$\mu$m and *D. willana* had the smallest at approximately 32$\mu$m (Fig. 3.5). *D. willana* eggs were approximately 3x and 2x smaller than *C. torulosa* and *H. banksii* respectively.

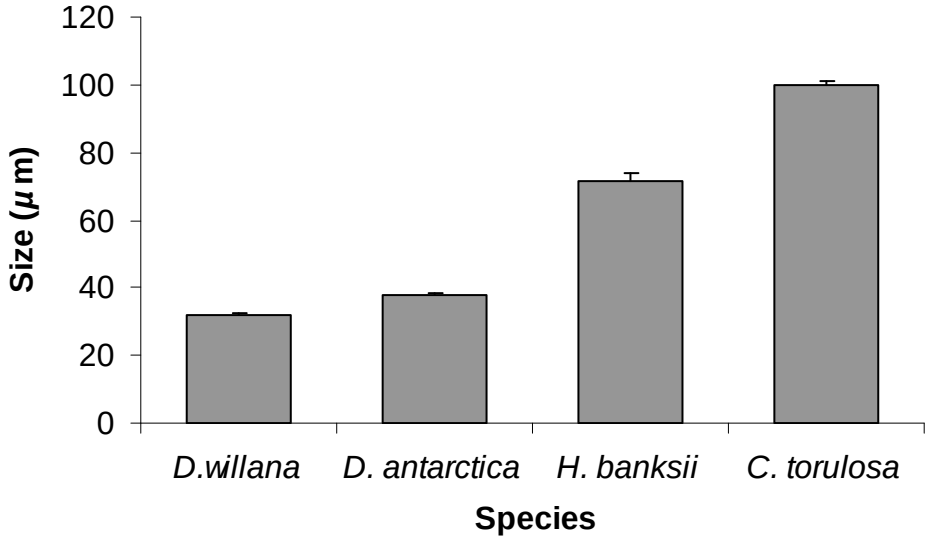


**Figure 3.5** Diameters of *D. antarctica*, *D. willana*, *H. banksii* and *C. torulosa* (*n*=30).

ANOVA of sinking rates showed a significant effect of species, but not of time (Table 3.2). Tukeys HSD test showed no significant difference between *D. antarctica* and *D. willana*, but there were significant differences between the two *Durvillaea* species and *H. banksii* and *C. torulosa*, and between *H. banksii* and *C. torulosa* (Figure 3.6). *C. torulosa*, which had the largest eggs, sank fastest at just over 1 mm $s^{-1}$. *D. antarctica* sank the slowest at approximately 0.1 mm $s^{-1}$. *D. willana*, *H. banksii* and *C. torulosa* sank approximately 2x, 6.5x and 11x as fast as *D. antarctica* respectively. There were no significant differences in sinking rates of eggs and zygotes of *H. banksii*.

**Table 3.2** ANOVA results of sinking rates across species and time. Time was treated as a random factor. Cochran's test was significant but data transformation could not stabilize variances so raw data were used.

| Source of variation | *df* | MS | *F* | *p* |
|---|---|---|---|---|
| **Species** | **3** | **5.91178** | **26.06098** | **0.011925** |
| Time | 1 | 0.32885 | 1.44969 | 0.314912 |
| Species x time | 3 | 0.22684 | 1.52664 | 0.211518 |
| Error | 112 | 0.14859 | | |

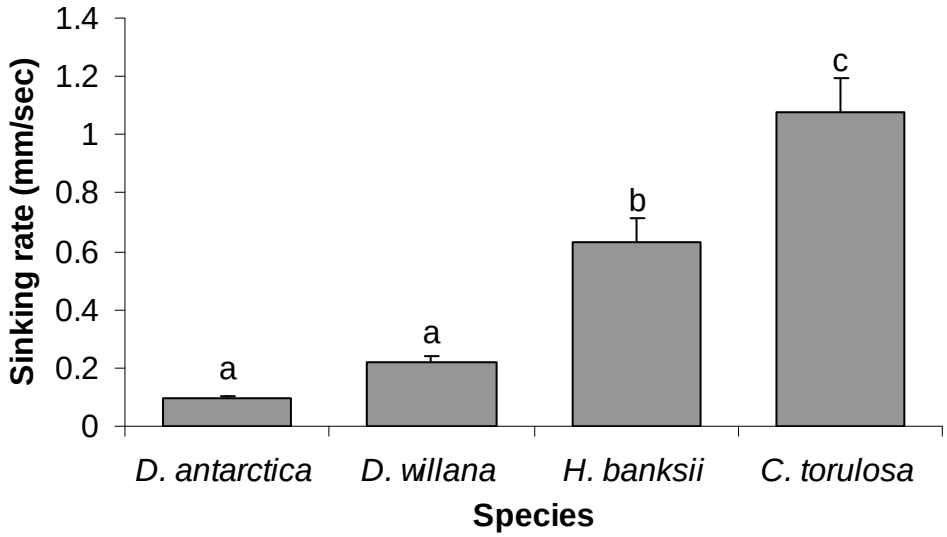


**Figure 3.6** Average sinking rates (+1s.e.) of *D. antarctica*, *D. willana*, *H. banksii* and *C. torulosa*. Labels with different letters indicate significant differences between average sinking rates (Tukey HSD, $p<0.001$) ($n=30$).

### 3.3.2 *Durvillaea* spp. dispersal

For the upshore dispersal experiments at Paratitahi and Seal Reef, there were significant differences in settlement densities between sampling times and distances from source populations (Table 3.3, Figs. 3.7, 3.8 and 3.9). Average settlement densities at distance from the populations were similar between sites (Fig. 3.7). Dispersal curves of *Durvillaea* spp. showed peaks in settlement at a distance of 0.1 – 0.6 m from the population. Settlement declined at greater distances but was often high (100-200 propagules per $cm^2$) 8 m from the

source at both sites (Figs. 3.8 and 3.9) At Seal Reef, settlement densities were a maximum of 15 propagules per $cm^2$ at 32 m (Fig. 3.9). Sample times with higher settlement densities had sharper declines in densities with increasing distance from the source.

**Table 3.3** ANOVA results of *Durvillaea* spp. settlement densities at different sampling times, with distance from populations at Paratitahi and Seal Reef. Time was treated as a random factor. Cochran's tests were significant and log-transformation of the data stabilized variances.

| Site | Source of variation | *df* | MS | *F* | *p* |
|---|---|---|---|---|---|
| Paratitahi | **Time** | **3** | **2.9367** | **27.68158** | **0.000000** |
| | **Distance** | **7** | **0.4901** | **4.65163** | **0.002404** |
| | Time x distance | 21 | 0.1050 | 0.88709 | 0.606649 |
| | Error | 56 | 0.1183 | | |
| Seal Reef | **Time** | **6** | **4.4229** | **54.0602** | **0.000000** |
| | **Distance** | **9** | **5.3723** | **65.4714** | **0.000000** |
| | Time x distance | 52 | 0.0817 | 0.3813 | 0.999964 |
| | Error | 269 | 0.2143 | | |

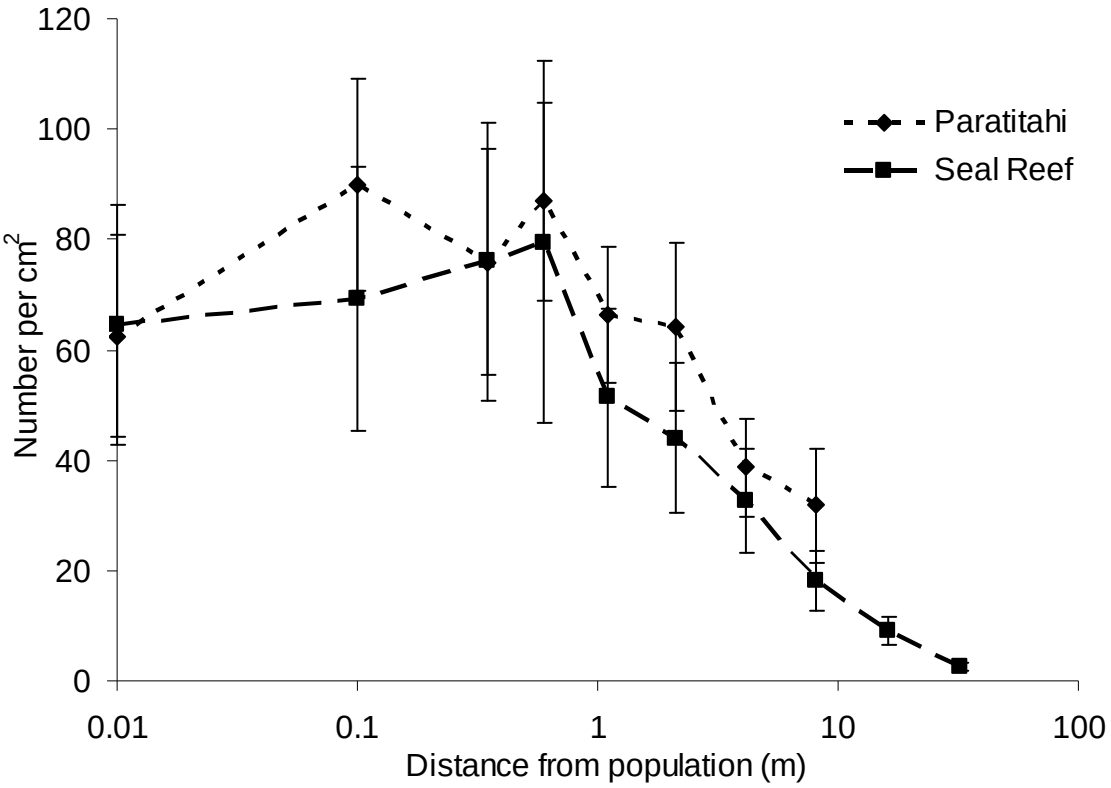


**Figure 3.7** Dispersal curves of *Durvillaea* spp. upshore dispersal experiments at Paratitahi and Seal Reef. Data are average number (+1s.e.) of propagules per $cm^2$ over all sampling times.

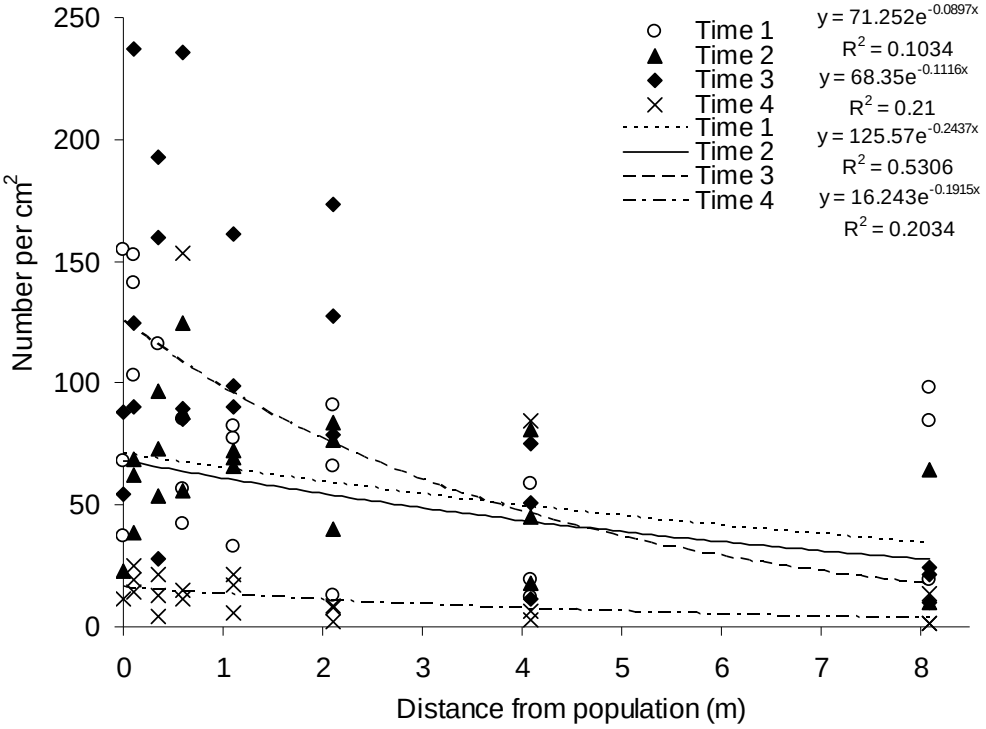


**Figure 3.8 *Durvillaea* spp., upshore dispersal experiment, Paratitahi.** Settlement of *Durvillaea* spp. with increasing distance upshore from the Paratitahi population at different times. Each data point is the average settlement per $cm^2$ per plate ($n$=3). Regression lines are exponential.

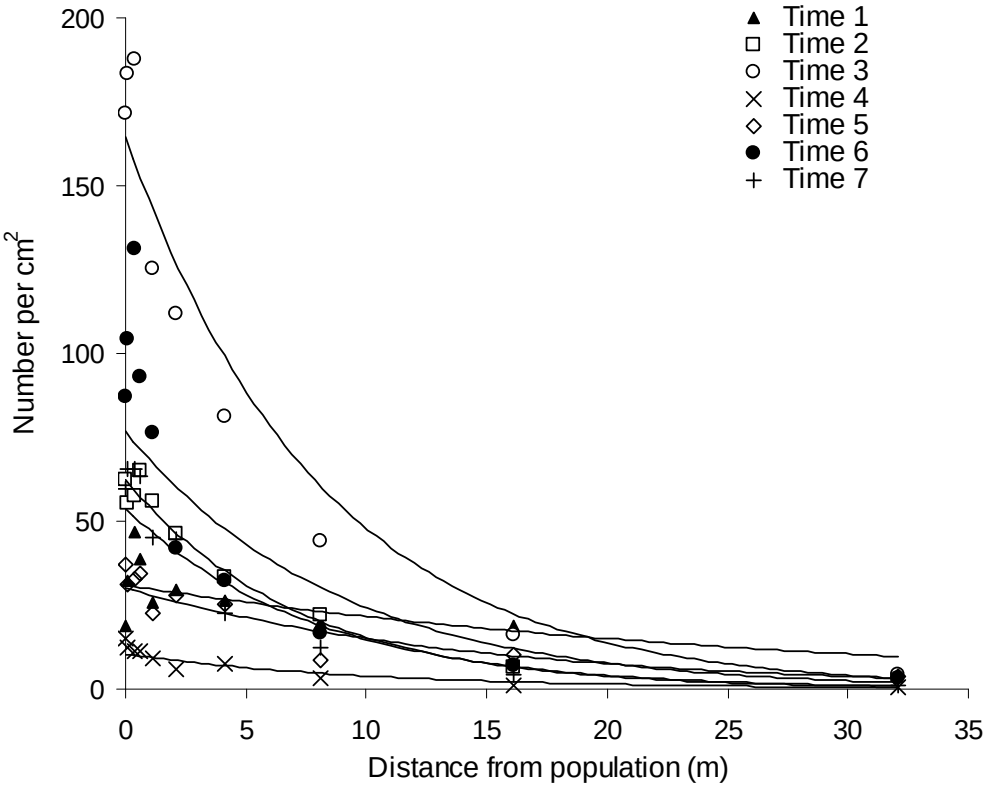


**Figure 3.9 *Durvillaea* spp., upshore dispersal experiment, Seal Reef.** Settlement of *Durvillaea* spp. with increasing distance upshore from the Seal Reef population at different times. Each data point is the average settlement per $cm^2$ over all replicate plates ($n$=5). Regression lines are exponential.

In the experiment that tested dispersal on a vertical surface, there was a significant time x distance interaction (Table 3.4). This was due to a larger decline in densities with distance on the first sampling time, but little difference in densities with distance at the two later sampling times (Fig. 3.10). Over all sampling times, very few propagules settled at 0.6-1.1 m, with a maximum of only 4 propagules per $cm^2$.

**Table 3.4** ANOVA results of *Durvillaea* spp. settlement densities at different sampling times with increase in distance vertically from a population at Seal Reef. Time was treated as a random factor.

| Source of variation | *df* | MS | *F* | *p* |
|---|---|---|---|---|
| Time | 2 | 61.0607 | 2.563099 | 0.137630 |
| Distance | 4 | 55.9262 | 2.335083 | 0.142623 |
| **Time x distance** | **8** | **24.1388** | **5.419228** | **0.003024** |
| Error | 14 | 4.4543 | | |

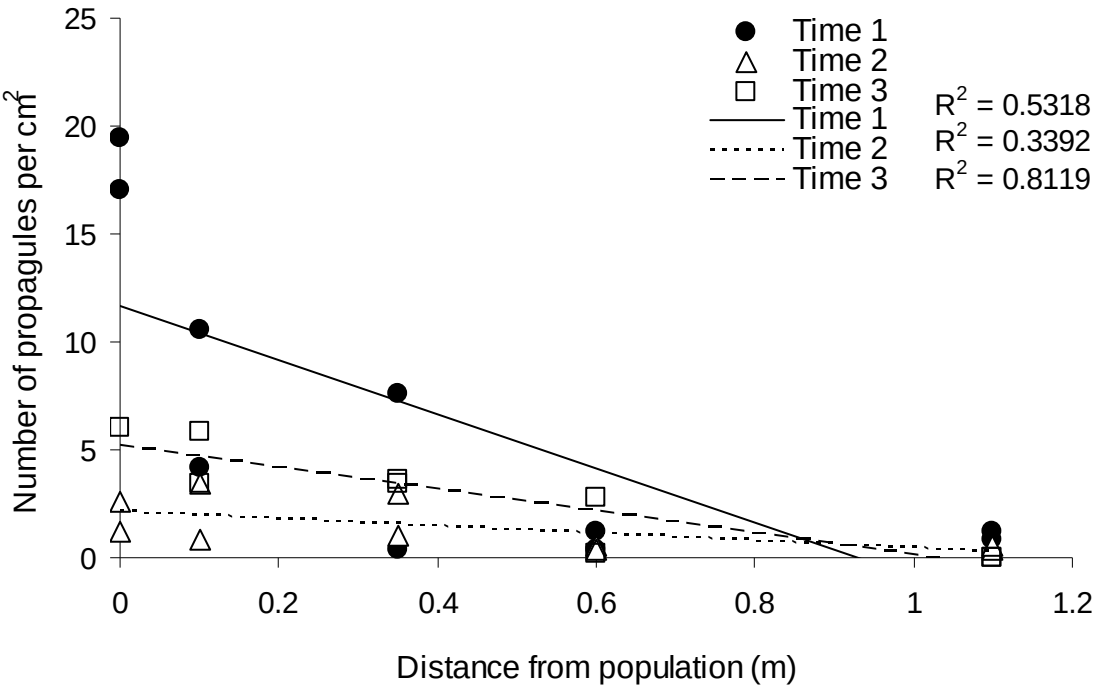


**Figure 3.10 *Durvillaea* spp., vertical rock face experiment.** Settlement of *Durvillaea* spp. with increasing distance from a population on a vertical rock face. Each data point is the average settlement per $cm^2$ per plate ($n$=2). Regression lines are linear.

### 3.3.3 *Hormosira banksii* dispersal

Settlement densities of *H. banksii* were significantly different between sites and there was a significant site x distance interaction (Table 3.5, Fig. 3.11). Overall, densities were highest within 0.35 m of the population, and low densities of less than approximately 10 propagules per $cm^2$ were recorded at distances 0.6, 1.1 and 2.1 m from the population.

Settlement at Wairepo at different times was significantly different between sampling time, and distance from the source population (Table 3.6, Fig. 3.12). Higher settlement occurred within 0.35 m of the population.

**Table 3.5** ANOVA results of *H. banksii* settlement densities at different sites with increase in distance from a population. Site was treated as a random factor. Variances could not be stabilised.

| Source of variation | *df* | MS | *F* | *p* |
|---|---|---|---|---|
| **Site** | **2** | **30.8510** | **14.31246** | **0.001023** |
| Distance | 5 | 2.8358 | 1.32135 | 0.326941 |
| **Site x distance** | **10** | **2.2091** | **2.19126** | **0.019807** |
| Error | 196 | 1.0081 | | |

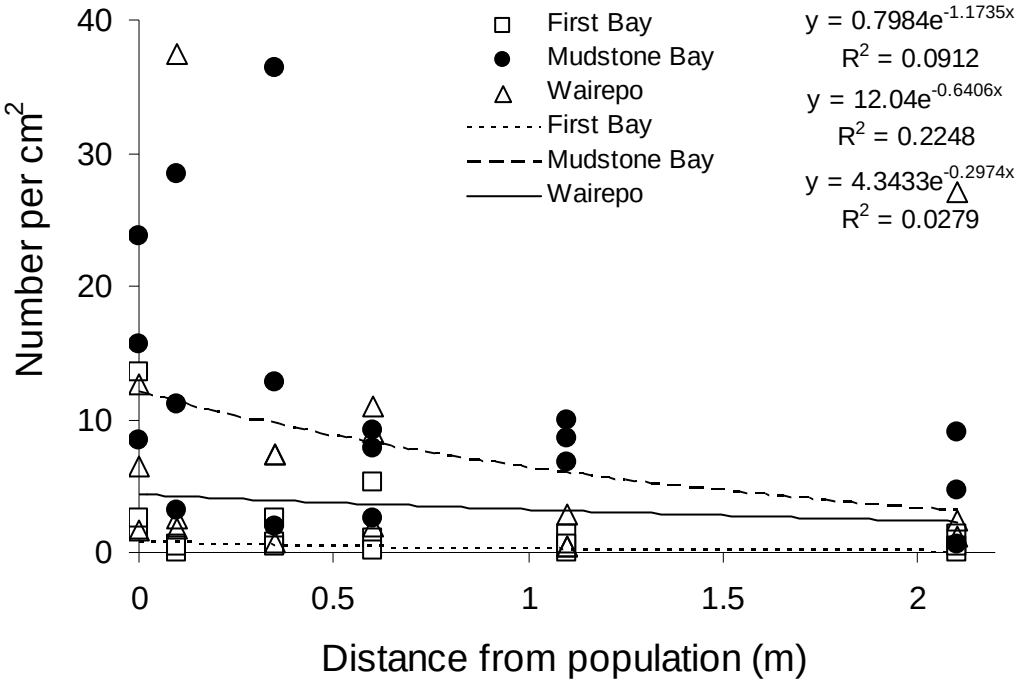


**Figure 3.11 *H. banksii*.** Settlement of *H. banksii* with increasing distance from nearest plants at different sites. Each data point is the average settlement per $cm^2$ per plate ($n$=3).

**Table 3.6** ANOVA results of *H. banksii* settlement densities at different times with increase in distance from a population at Wairepo. Time was treated as a random factor. Variances could not be stabilised.

| Source of variation | *df* | MS | *F* | *p* |
|---|---|---|---|---|
| **Time** | **3** | **81.4616** | **54.93344** | **0.000000** |
| **Distance** | **5** | **6.2646** | **4.31145** | **0.009498** |
| Time x distance | 15 | 1.5077 | 1.45079 | 0.123487 |
| Error | 277 | 1.0393 | | |

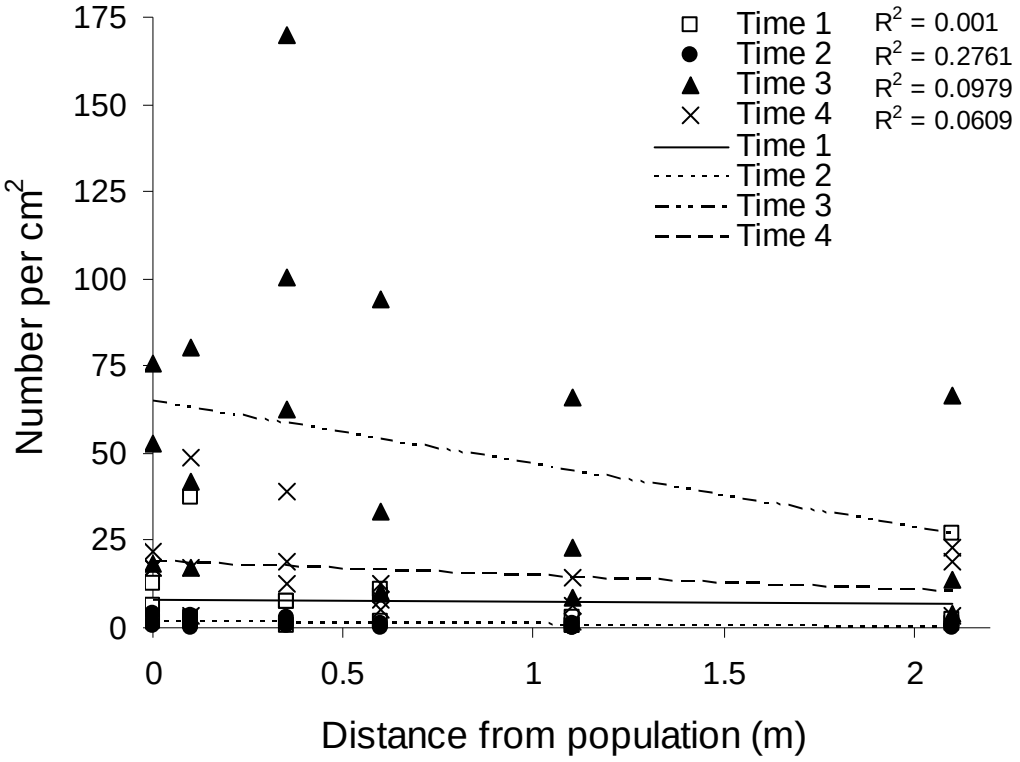


**Figure 3.12 *H. banksii*.** Settlement of *H. banksii* with increasing distance from nearest plants at Wairepo during different sampling times. Regression lines are linear. Each data point is the average settlement per $cm^2$ per plate (*n*=3).

### 3.3.4 *Fucus gardneri* dispersal

There were no significant differences in settlement numbers of *F. gardneri* at different times or distances (Table 3.7). However, a univariate test of significance for planned comparison of settlement under the canopy and all other distances showed that settlement was higher under an adult canopy, and was significantly lower outside (p=0.009501, Figure 3.13). Very low settlement densities occurred at 0.6 m and farther from the nearest plants. Settlement under the canopy was very patchy, and this was reflected in the highly variable germling numbers per $cm^2$, which ranged from 0 to 797 per $cm^2$.

**Table 3.7** ANOVA results of *F. gardneri* settlement densities at different times with increase in distance from a population at Fogarty Creek. Time was treated as a random factor. Variances could not be stabilised.

| Source of variation | *df* | MS | *F* | *p* |
|---|---|---|---|---|
| Time | 1 | 2531.250 | 0.787894 | 0.415389 |
| Distance | 5 | 4850.010 | 1.509648 | 0.331157 |
| Time x distance | 5 | 3212.677 | 0.914558 | 0.472994 |
| Error | 168 | 3512.821 | | |

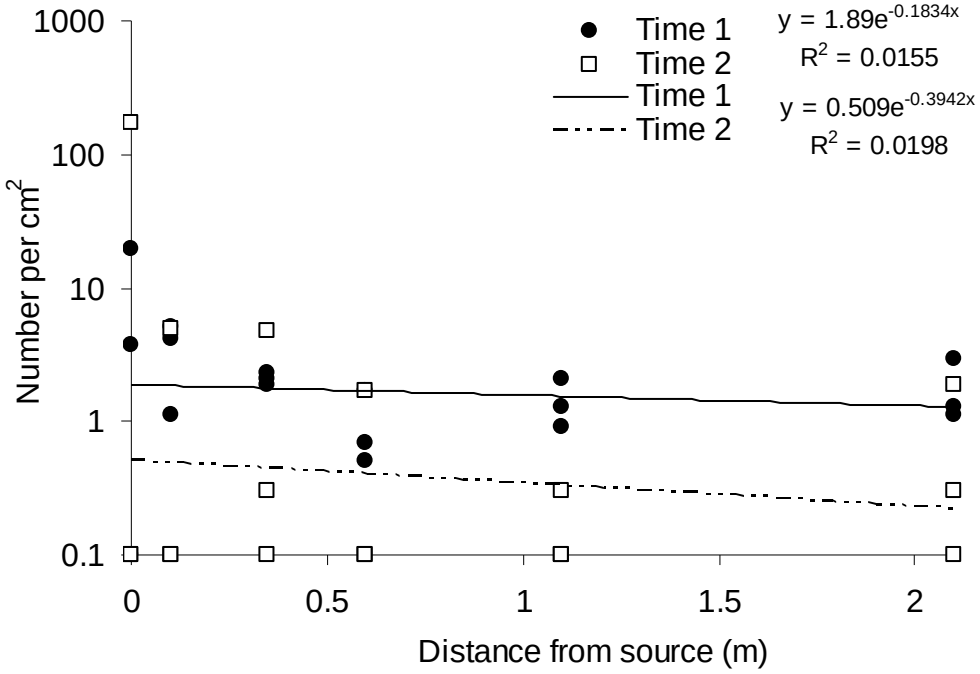


**Figure 3.13 *F. gardneri*.** Settlement of *F. gardneri* with increasing distance from nearest plants. Data points are averaged plate counts + 0.1 (*n*=3). Note log scale of y-axis.

### 3.3.5 *Cystophora torulosa* dispersal

High settlement densities were recorded directly under the source plants, but low densities occurred on all other plates. Settlement of *C. torulosa* declined with increasing distance from the source plants, but settlement was still observed 2 m from the source.

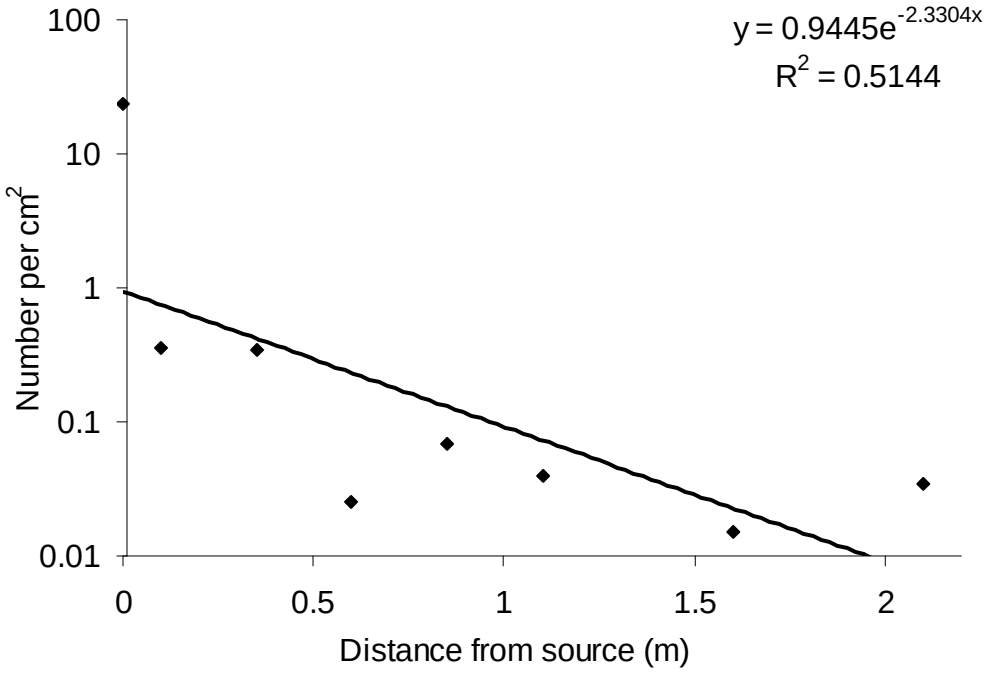


**Figure 3.14 *C. torulosa*.** Settlement of *C. tourlosa* with increasing distance from source plants. Data points are averaged plate replicates (*n*=4). Note log scale of y-axis.

### 3.3.6 Comparative dispersal

Plotting settlement data for each species showed large differences in densities between species (Fig. 3.15). For *Durvillaea*, a decline in densities did not occur until around 8 m from the source population. Other species had declines in settlement densities much closer to the sources, at around 0.5 m.

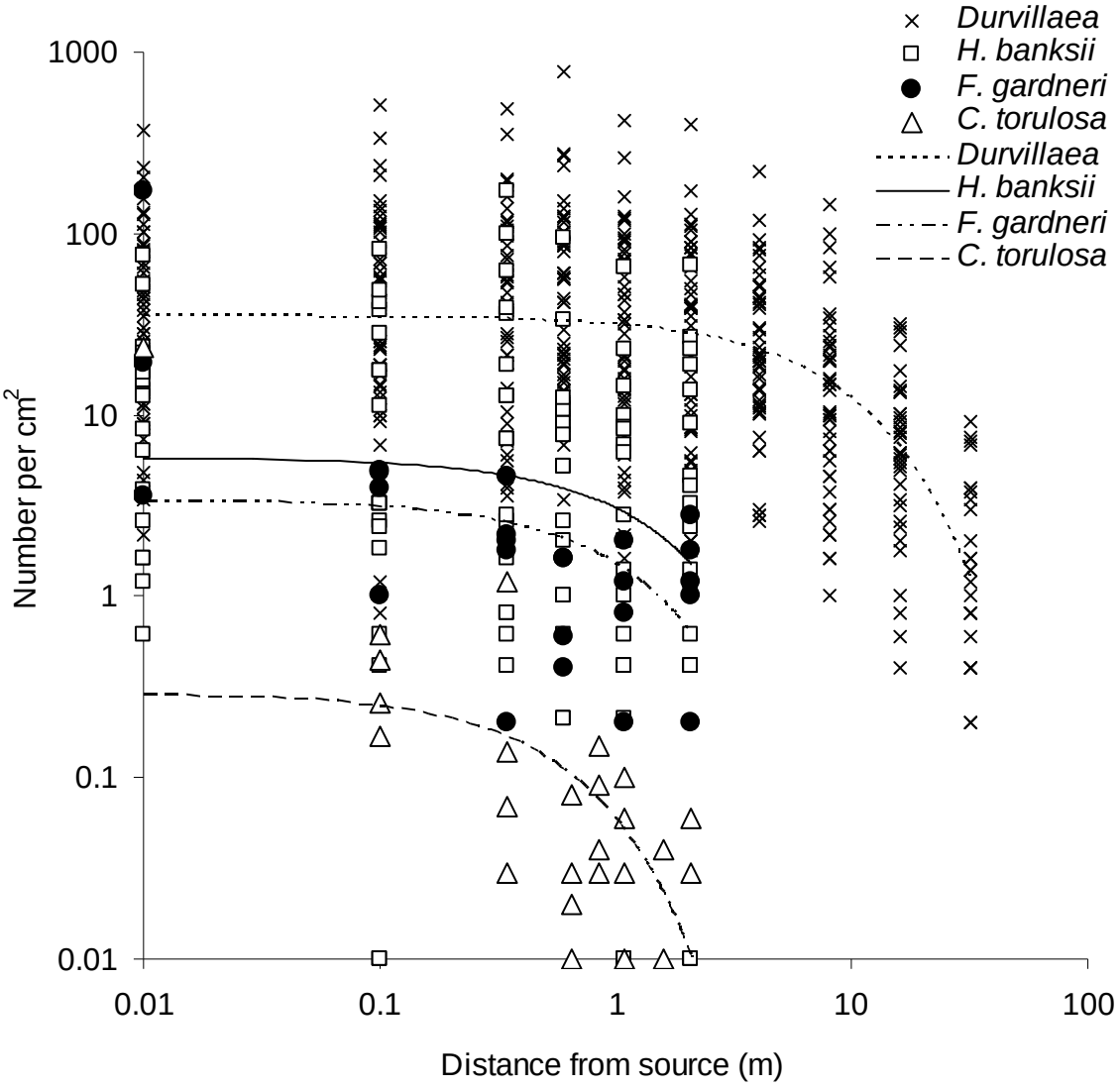


**Figure 3.15** Settlement of *Durvillaea* (*n*=47), *H. banksii* (*n*=18), *F. gardneri* (*n*=6) and *C. torulosa* (*n*=4) with increasing distance from nearest plants. Data points are averaged plate counts + 0.01, all sites and times included. Regression lines are exponential. Note log scales of x- and y-axes.

## 3.4 Discussion

### 3.4.1 Egg sizes and sinking rates

There were large differences in sizes of eggs and sinking rates between species. In agreement with previous studies on sinking rates (Coon et al. 1972, Okuda & Neushul 1981, Hoffmann & Camus 1989), this study found that in general, larger eggs sank faster than smaller eggs. *C. torulosa* had the largest eggs and sank the fastest, *Durvillaea* spp. had the smallest eggs and sank the slowest, and *H. banksii* had intermediate sized eggs and sinking rates. However, within *Durvillaea*, species did not conform to this general trend. *D. willana* had the smallest eggs (av. diam. 32 $\mu$m), but sank twice as fast as *D. antarctica* eggs (av. diam. 38 $\mu$m). *D. willana* eggs were either denser than *D. antarctica* eggs, or the mucilage layers surrounding the eggs were thinner. Thicker mucilage around *D. antarctica* eggs would result in the eggs being less dense, and sinking more slowly (Boney 1975, 1978).

The fast sinking rates of *C. torulosa* eggs would decrease the time spent in the water column, and as a result, their dispersal distances. In contrast, it is hypothesized that the small, slow-sinking eggs of *Durvillaea* spp. spend a longer time in the water column and this would enhance dispersal. In addition, *D. antarctica* eggs are shed with mucilage which was observed to be buoyant and remain at the water surface during the sinking rate experiment. It is possible that mucilage aids in dispersal in a similar way to that described for red algae by Boney (1978), in which mucilage strips containing spores remain buoyant, allowing the eggs to descend out of the mucilage over larger areas. In a pilot experiment, settlement plates were suspended from a wharf at Kaikoura at 1 m depth within approximately 5 m deep water (Dunmore, unpublished data). The nearest *D. antactica* plants were approximately 15 m away. *D. antarctica* eggs settled on these plates, indicating the eggs can remain in the upper water column, thereby enhancing their dispersal capability.

### 3.4.2 Dispersal

In general, fucoid algae have very short dispersal, most propagules being found to fall near the parent plants with an exponential decline in densities with distance (Kendrick & Walker 1991, Chapman 1995, Kendrick & Walker 1995, Johnson & Brawley 1998). In general, fucoids have maximum dispersal estimates of around 30 m (Chapman 1995, Dudgeon et al. 2001), but some species have dispersal estimates of less than 10 m (Bellgrove et al. 1997, van Tamelen et al. 1997, Bellgrove et al. 2004, McKenzie & Bellgrove 2006). It was expected that the species in this study would have similar, highly localised dispersal. Surprisingly, *Durvillaea* spp. showed much broader dispersal than was expected, with high settlement densities up to 8 m and lower settlement detected at 32 m from the nearest plants, which was

the maximum sample range of the study. This extensive dispersal is thought to be a result of the combination of small eggs, slow sinking rates and the presence of buoyant mucilage. Settlement on a vertical surface did appear to be more restricted, however, with very low propagule numbers at 1 m distances. Settlement on a vertical surface would be much more challenging than settlement on a horizontal one, especially in a fluid, turbulent environment.

Dispersal of *H. banksii*, *C. torulosa* and *F. gardneri* was much more restricted than *Durvillaea* spp. Settlement densities were much lower, and although settlement occurred 2 m from the nearest plants, settlement was higher within 0.5 m. This short range dispersal is in accordance with other studies on fucoids (Kendrick & Walker 1991, Kendrick & Walker 1995, Serrao et al. 1997, van Tamelen et al. 1997, Johnson & Brawley 1998, McKenzie & Bellgrove 2006). For example, around 98% of propagules settled within 1m of parental *S. muticum*, and densities declined exponentially with distance from source (Kendrick & Walker 1991, 1995). Dispersal of propagules of *Silvetia compressa* (previously *Pelvetia compressa*) is also highly localised with settlement 1-2 orders of magnitude higher under the adult canopy (Johnson & Brawley 1998).

The limited propagule dispersal of *H. banksii* in this study is similar to the maximum of about 10 m estimated previously (Bellgrove et al. 1997, Bellgrove et al. 2004, McKenzie & Bellgrove 2006). Greater settlement was found under an adult canopy, and reduced settlement outside canopies and in bare patches (Chapter 2). Dispersal experiments found highest settlement within 0.35 m of the source plants. Sites and times with greater settlement densities displayed a stronger decline in densities with increasing distance from the source plants.

Van Tamelen *et al.* (1997) stated that *F. gardneri* eggs rarely travel more than 0.5 m from the parental plant. Other studies have reported a dispersal radius of less than 1 m (see Stekoll & Deysher 2000, Driskell et al. 2001). This study showed that settlement occurred 2 m from the nearest plant, but settlement was usually much greater under an adult canopy. *F. gardneri* sheds gametes during low tide, along with copious amounts of viscous mucilage that can transport gametes directly to the substrate and decreases dispersal. This may account for the patchy distribution of propagules on plates under canopies, where densities were highly variable within plates. Eggs that were carried to the substrate in dripping mucilage probably did not disperse from their initial point of contact, resulting in patchy occurrences of very high density settlement (maximum 797 per $cm^2$).

*C. torulosa* dispersal was also very restricted with settlement occurring 2 m from the source and at very low densities. However, this experiment did not replicate natural conditions because plants were enclosed in a mesh bag and attached over a settlement plate. Normally plants would float higher in the water column, and the larger propagule source from

a population would lead to higher settlement densities. Nevertheless, it is expected that dispersal would still be restricted due to the fast sinking rates of the eggs.

The species studied here produce gametes in conceptacles that are distributed over either the entire thallus or the tips of the thallus. The algae are buoyant, and thus larger species like *Durvillaea* spp. may have greater dispersal shadows than smaller species because eggs would be released higher in the water column. However, this would be effective only if gametes are either shed when plants are submerged, or if some gametes are retained on the plants during the incoming tide and their release occurs after submergence. Gamete release in all study species was observed during low tides, and since these fucoids may release gametes during calm conditions as reported for other fucoids (Pearson & Brawley 1996, Serrao et al. 1996, Pearson & Brawley 1998, Pearson et al. 1998), the gentle wash of the incoming tide may introduce gametes to the substratum very quickly. It is unknown whether gametes are washed from the plants immediately, if some gametes are held by sticky mucilage on the parent plant until submerged, or if gamete release also occurs during high tide. This information would be valuable because such details of gamete release must influence dispersal enormously by affecting the amount of time gametes remain in the water column.

With the exception of *Durvillaea* spp., the species studied in this chapter exhibited fairly restricted dispersal capabilities, and it is predicted that this would slow their recovery from large-scale disturbances. However, on a local scale, their dispersal is sufficient to transport propagules to different shore heights and habitats, and thus lack of supply is not a reason for their patchy or restricted vertical distributions. Post-settlement mortality appears to have much stronger effects on their survival patterns. This is examined in Chapter 4. Despite their localised dispersal of propagules, long distance dispersal is possible via the detachment and drifting of adult plants, and subsequent release at a distant site. However, this method of dispersal may not always produce viable offspring, especially for dioecious species that require a male and female plant to arrive in fairly close proximity to each other to ensure fertilisation success. In addition, most drift algae end up as beach cast, high on the shore. Even if fertilisation is successful, transport to a suitable habitat may not be.

Further experiments examining settlement farther from source plants would enhance our knowledge of dispersal limits. This study did not aim to determine dispersal limits, rather it examined the differences in settlement densities with increased distance from populations. For all species, settlement densities declined with increasing distance from the nearest plants, and this was variable on a temporal scale. Mortality of early post-settlement algae is extremely high (Vadas et al. 1992), and therefore settlement of abundant propagules is generally required for successful recruitment and to produce viable adult populations (Schiel

2004). High densities of germlings may reduce desiccation and heat stress (Hruby & Norton 1979, Ang & DeWreede 1992, Viejo et al. 1999), and swamp areas so that they may escape grazing (Lubchenco 1983, Vadas et al. 1992, Underwood 1998). Short dispersal may significantly reduce species abilities to reach critical settlement thresholds at greater distances from their source, and this would influence range expansion, gene flow and recovery from disturbance.

# Chapter 4
# Early post-settlement survival and growth across shore heights

## 4.1 Introduction

### *Supply and germling survival*

Larval and propagule supply and dispersal are core elements in the establishment, maintenance and stability of populations. The distance larvae and propagules are spread from their source and their abundance at settlement has considerable impact on population structure, connectivity, genetic make-up, and response to disturbances. There has been considerable re-emphasis on larval and propagule supply and early life stage survival, and how differences among taxa can drive major components of rocky reef communities (Underwood & Denley 1984, Underwood & Fairweather 1989, Brawley & Johnson 1991, Underwood 1991, Davison et al. 1993, Schiel 2004). Fine scale differences in larval behaviour, and tolerances to biotic and abiotic stresses during dispersal, settlement and early post-settlement stages can lead to large scale differences in recruitment. Early life stage information is lacking for many dominant organisms; in particular, there is a general lack of field-based data on early life stages of algae (<1 mm) (Chapman 1995, Schiel & Foster 2006). The difficulty of studying microscopic stages and controlling factors in field experiments has led to many laboratory experiments, but it is essential to combine knowledge from both field and laboratory studies for a fuller understanding of ecological processes affecting early life stages.

The early post-settlement or germling stages of algae are particularly vulnerable, as germlings do not have the physical attributes and adaptations of larger plants to withstand harsh environmental conditions. Also, their microscopic size and lack of strong chemical defences make them easy targets for the multitude of grazers that inhabit rocky shores. Extremely high mortality rates have been reported for early post-settlement stage of algae, with only a fraction of settlers successfully recruiting to a population (Chapman 1984, 1986, Santelices 1990, Ang 1991, Vadas et al. 1992, Kendrick & Walker 1995, Viejo et al. 1999, Ladah et al. 2003, Wright et al. 2004, Dudgeon & Petraitis 2005, Schiel & Foster 2006). In studies of fucoid algae, Miller and Vadas (1984) found nearly 100% mortality of newly settled *Ascophyllum nodosum* germlings within 2 months, and Ang (1991) determined that only 0.4 to 12% of newly settled *Fucus distchus* germlings survived to become macro-recruits. Kelp survival is also very low; Chapman (1984) investigated survival of the laminarians *Laminaria digitata and L. longicruris* and estimated that chances of surviving from a microscopic benthic plant to visible size were 1 in half a million and 1 in 9 million respectively (0.0002 and 0.00001%). A multitude of physical and biological factors influence growth and survival of newly settled algae (see reviews by Santelices 1990, Vadas et al. 1992,

Chapman 1995). In particular, desiccation, temperature and grazing have been identified as major factors affecting intertidal germlings.

***Heat/desiccation stress***

Desiccation and thermal stress are not only important sources of mortality of germlings, but also can have sublethal effects by slowing or halting photosynthesis and development (Baker 1909, 1910, Hay 1979, Schonbeck & Norton 1980a, Smith & Berry 1986, Brown 1987, Davison *et al.* 1989, Chapman & Johnson 1990, Brawley & Johnson 1991, Davison 1991, Davison *et al.* 1993). The combination of hot, dry weather with low tides, especially those of long duration, can be particularly stressful for newly settled germlings (Schonbeck & Norton 1978, Schonbeck & Norton 1980a). Germlings that settle at shore levels higher than where they originate may be especially vulnerable. Species normally inhabiting lower levels of the shore are less tolerant of desiccation and thermal stress than those inhabiting higher levels (Baker 1909, 1910, Zaneveld 1937, Schonbeck & Norton 1978, Dring & Brown 1982, Oates & Murray 1983, Davison & Pearson 1996, Li & Brawley 2004, Skene 2004), and parental thermal history can affect embryo heat tolerance (Li & Brawley 2004). This greatly influences species vertical distributional limits, and intra- and inter-specific interactions. For example, eggs or embryos originating from low-shore plants that have non-stressful thermal histories will be intolerant of desiccation. If they disperse to the mid-shore they may experience high mortality or suffer sub-lethal stress that affects their growth and subsequent competitive interactions.

Desiccation does not always have a negative effect on algae; growth and survival of some algae is enhanced by a degree of emersion. Schoenbeck and Norton (1980b) and Rugg and Norton (1987) transplanted the high shore fucoid *Pelvetia canaliculata* to the low shore. Initially the plants grew well, but eventually decayed and died as a result of prolonged submergence. Wright *et al.* (2004) found that, in contrast to their expectations, performance (determined by growth, reproduction and/or survival) of transplanted *Fucus gardneri* embryos, juveniles and adults was not always worse in the high zone than in the mid zone, even in months when exposure time was greatest.

***Grazing***

The sub-lethal stress that germlings experience due to desiccation, thermal stress or increased submergence can influence competitive and grazing interactions (Davison et al. 1993). For example, slower growth of germlings experiencing sub-lethal stress can give competitors an advantage while increasing their exposure to grazing because they take longer to reach a size refuge. Grazing is undoubtedly a large source of mortality for many germling algae (see reviews by Santelices 1990, Vadas et al. 1992), but it has also been shown to have weak or

positive effects. Grazing can be a major structural influence, but its effect is dependent on the situation because grazing is temporally and spatially variable.

Many studies have shown that grazing can vary with season (Underwood & Jernakoff 1984), latitude (Jenkins et al. 2005), vertical position on the shore (Chapman & Johnson 1990), and the species, size and abundance of grazers and algae (Lubchenco 1978, Underwood & Jernakoff 1981, Lubchenco 1983, Barker & Chapman 1990, Cervin & Aberg 1997, Lotze et al. 2000). For example, Chapman and Johnson (1990) found that grazing had little effect on *Fucus* species in the low shore, but this increased with increasing shore height. Cervin and Aberg (1997) found that grazing on *Ascophyllum nodosum* by *Littorina* species was effective only at high densities. Lubchenco (1983) found that small (1-3cm long) *Fucus* were more susceptible to grazing by gastropods than medium (5-7 cm long) recruits. Positive effects of grazing occur when grazers reduce ephemeral algal cover, enabling perennial algae to recruit (Lubchenco 1978, Lubchenco & Menge 1978, Lubchenco 1983, Kim 1997, Worm et al. 1999, Worm et al. 2001). Clearly the effects of grazing are highly variable; it is therefore essential to obtain information on grazing at different times on a number of shores using several species before any generalisations concerning the influence of grazing in structuring intertidal communities can be proposed.

***Distributional limits***

In addition to having high post-settlement mortality that limits their recruitment, algae are generally considered to have very limited gamete/propagule dispersal compared to other taxa (reviewed by Santelices 1990), and this is thought to limit their local-scale distributions and large scale range expansion. However, many studies have determined dispersal by examining recruitment patterns (Anderson & North 1966, Deysher & Norton 1982, Arrontes 1993) and did not take into account the high post-settlement mortality that can occur with increasing distance from source populations. Biological and physical stresses can change on very small spatial scales, and dispersal away from a source can take propagules outside favourable habitats. By examining recruitment patterns, dispersal distances can be underestimated, and subsequent studies have found some species have far wider dispersal of gametes than previously thought (Reed et al. 1988, Reed et al. 1992, Dudgeon et al. 2001, Gaylord et al. 2002, Reed et al. 2004). It appears that at least on a local scale (tens of meters), algae have the potential to settle further than their observed distributions, and early post-settlement mortality may be more important than dispersal in determining local scale recruitment patterns (Johnson & Brawley 1998, Dudgeon et al. 2001).

New Zealand and Oregon are at approximately the same latitude in the southern and northern hemispheres with long stretches of rocky intertidal shores and an abundance of

fucoid seaweeds. However, their tidal regimes and intertidal community structures are very different. In New Zealand, tides are semidiurnal; two high and two low tides occur each day and are of equal magnitude. In Oregon, tides are mixed semidiurnal with different amplitudes. High-high and low-low tides are followed by low-high and high-low tides. During summer the low-low tides can occur during daytime, which can exert tremendous stresses on intertidal communities because they are emersed for very long periods.

On exposed shores of the east coast of New Zealand, the high shore zone is dominated by bare space and grazers, and the mid and low zones are dominated by perennial algae. In contrast, Oregon has high- and low-shores zones dominated by many species of perennial and ephemeral algae, and mid shore zones dominated by mussels and barnacles. In New Zealand, *H. banksii* is the only midlittoral fucoid and dominates the mid to low shore levels of sheltered areas (Morton & Miller 1968). It does not extend its range into the high shore, but is found in small patches amongst *Cystophora* spp. and *Carpophyllum maschalocarpum* on the low shore. *D. antarctica* dominates the low shore at wave-exposed sites, and does not extend into the mid shore. At wave-exposed sites in Oregon, *P. limitata* and *F. gardneri* are abundant on the high shore (Abbott & Hollenberg 1976). Isolated plants of *F. gardneri* are found on the low shore, but *P. limitata* is restricted to the high shore.

The reasons for these distinct distribution patterns in New Zealand and Oregon are not intuitively obvious. A small number of studies has attempted to explain limits, but were often at single sites and/or at one time. In New Zealand, Hay (1979) showed that with removal of limpets, the distribution of *D. antarctica* could temporarily be extended up the shore at one site, but not at another. He determined that, ultimately, vertical limits were set by desiccation. In Washington, U.S.A., Pollock (1969) transplanted *F. gardneri* germlings into high and low zones and found no difference in survival. He concluded that there were no adverse physiological effects of transplanting to different zones. However, temporal variation in environmental and biological conditions, and interactions of these conditions with different developmental stages, can influence survival and growth (Brawley & Johnson 1991, Wright et al. 2004).

***Experimental testing***

Previous chapters have shown that species such as *Hormosira banksii* and *Durvillaea antarctica* have the ability to settle outside their observed adult vertical distributions. Settlement along a vertical gradient exposes germlings to a gradient of heat and desiccation stress, and also to variable grazing pressure. This chapter examines the consequences of fucoid algae settling at different shore heights in New Zealand (using *Hormosira banksii* and *Durvillaea antarctica*) and Oregon (using *Fucus gardneri* and *Pelvetiopsis limitata*).

Experiments investigated vertical distributions of these species by examining the relative importance of grazing and heat/desiccation stress in influencing early post-settlement survival and growth, and comparing these between species. Fucoid algae have several characteristics that make them excellent model organisms for experimentation on their early life stages. They are abundant, often fertile over long periods and are usually easy to manipulate to release gametes, fertilise and settle onto artificial substrates in preparation for outplanting. They also have relatively large propagules and simple life cycles with no alternation of generations.

A fully balanced experiment was designed to test the effect of grazing, heat stress/desiccation, and shore height on the survival and growth of germlings, and this was repeated at different times of the year to obtain seasonal comparisons. The null hypotheses were: 1) the survival and growth of germlings does not differ across shore heights, 2) grazing has an equal effect on germling survival across shore heights, and 3) the provision of shade (alleviating a degree of heat stress and desiccation) does not affect the growth and survival of germlings across shore heights. These experiments on localised processes which determine species distributions and abundances give an insight into regional processes dictating species ranges.

## 4.2 Methods

### 4.2.1 Sites and tidal cycles

The two sites in New Zealand were located in the South Island on Kaikoura Peninsula (Fig. 4.1). They were Seal Reef (42° 25' S, 173° 43' E) and First Bay (42° 25' S, 173° 42' E), semi-exposed mudstone platforms approximately 200 metres apart. *D. antarctica* and *H. banksii* naturally occur in distinctly exposed and sheltered conditions respectively, so germlings were not transplanted outside their normal wave-exposure habitats. The effect of wave exposure was examined in a separate, concurrent experiment (Taylor 2002). Therefore, *D. antarctica* plates were placed into exposed situations, and *H. banksii* plates were placed in sheltered areas (e.g., behind rocky outcrops that sheltered plates from the full force of waves).

The two sites in Oregon were Depoe Bay (44° 48' N, 124° 03' W) and Fogarty Creek (44° 51' N, 124° 03' W), basaltic semi-exposed platforms approximately 3.5 km apart (Fig. 4.2). *F. gardneri* and *P. limitata* occurred in the same wave exposure, so germlings were transplanted into the same areas.

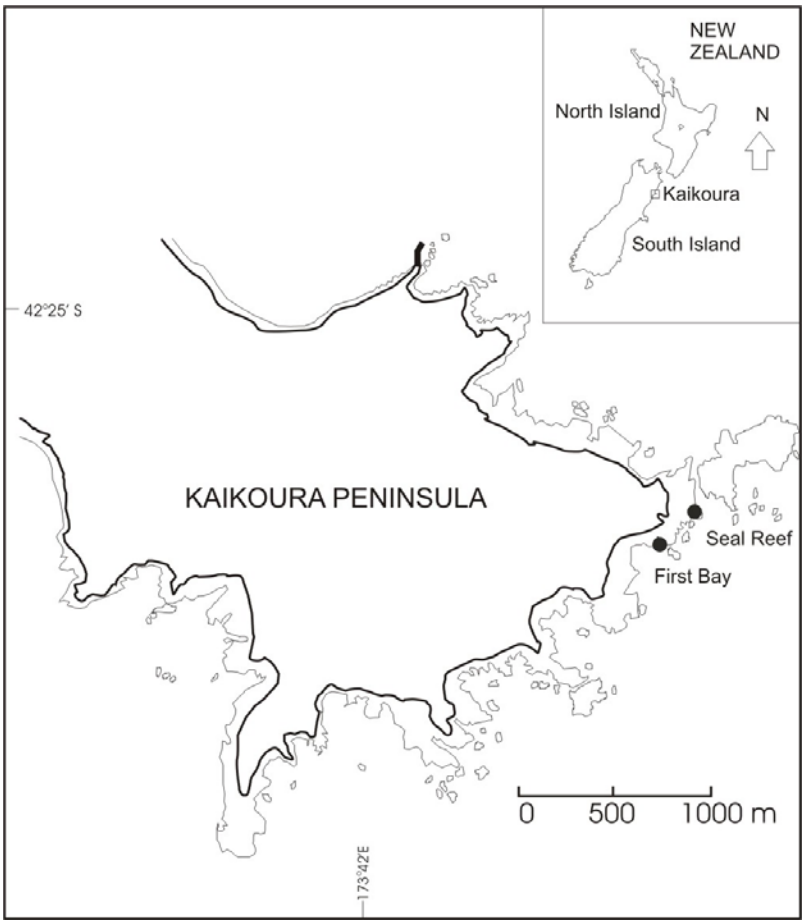


**Figure 4.1.** Map of Kaikoura Peninsula showing study sites and location within New Zealand.

Three tidal zones were identified at each site, characterised by distinct changes in algal and sessile invertebrate composition and abundance. Zones in New Zealand were 1.7m, 1.0m and 0.45m above chart datum for high, mid and low zones respectively. Oregon zones were 1.8m, 1.3m and 0.2m above chart datum for high, mid and low zones respectively. These heights were based on maximal tidal ranges and normal distributions of each species. Five haphazard 0.25m$^2$ quadrats were monitored in each zone at each site to describe the habitats. Percent covers of algae and sessile invertebrates were estimated, and numbers of mobile invertebrates were counted. Loggers recorded temperature at each tidal level every 30 minutes. Data were plotted to show differences in temperature at each tidal height, and were also used to determine emersion times. Dynamometers (Bell & Denny 1994) were placed in the low shore at each site and were checked at each sampling period to determine the wave climate.

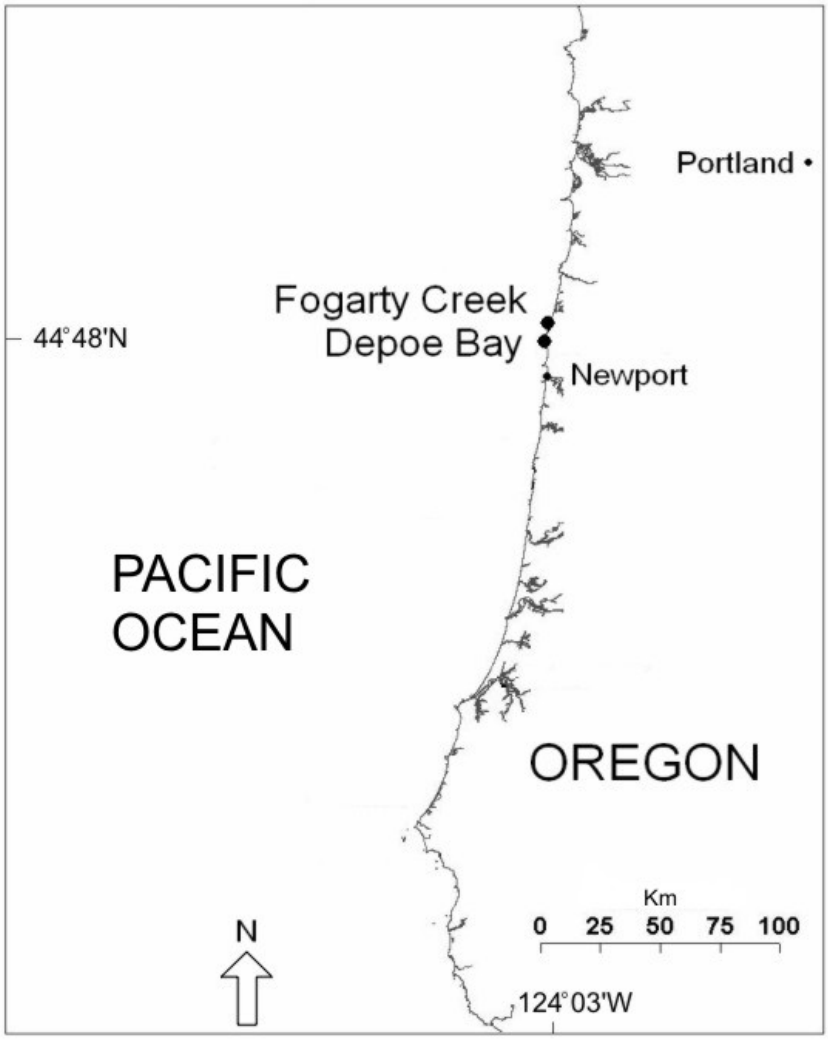


**Figure 4.2.** Map showing study sites in Oregon, U.S.A..

### 4.2.2 Experimental design

Embryos were settled onto artificial plates as described in section 4.2.3 below, in preparation for transplantation into the field. Artificial plates were used in favour of natural rock surfaces because they provided a standard substrate on which microscopic germlings could be distinguished. Previous experimentation showed that the plates were a good substrate for algal settlement and recruitment (Chapter 2; Schiel, unpublished data). The fibrolite ('Hardiflex™') plates were 11 x 11cm and 7mm thick, with a hole in the centre to enable attachment to the substratum by a stainless steel screw that was inserted into a plastic rawl plug in the rock.

Plates were randomly assigned to five grazing and heat stress/desiccation treatments, and each treatment had 3 replicates. Treatments were: fence, fence control, open, fence + shade, and fence control + shade (Fig. 4.3). To test the effects of grazing, plates were enclosed in stainless steel mesh fences to prevent access by gastropods ('fence'), enclosed in fences which had sections cut from the sides to allow grazer access but still allowed any effects of the fence ('control'), and not fenced ('open'). To test the effect of reducing heat

stress/desiccation, plates were enclosed in fences and controls which had shadecloth on top ('fence + shade' and 'control + shade' respectively). Plates were placed in high, mid and low zones at each site, and were recessed into the rock to ensure they were flush with the substratum.

The fences were approximately 11 x 11cm and 4cm high, with a 2cm lip turned outwards at the top. The mesh hole size was 2 x 2mm. These fences were effective in preventing large invertebrates from accessing the plates, but some very small invertebrates such as snails, amphipods and isopods were occasionally seen inside the fences. Fences with shadecloth prevented grazing and alleviated a degree of heat stress/desiccation, and fence controls + shade allowed grazer access but still had effects of the fence and shade. Shadecloth was two layers of flyscreen mesh that shaded the plates by approximately 50%. During four experiments (*H. banksii* summer and autumn, *D. antarctica* winter and *P. limitata* spring) temperature loggers were placed in one fence and one fence + shade treatment to determine the difference in temperature when plates were shaded. Temperature was recorded every 30 minutes.

**Figure 4.3.** Grazing and heat/desiccation treatments: fence (top left), fence + shade (top right), open (bottom left) and fence control (bottom right) treatments in the field in Oregon, U.S.A.

A binocular microscope was used to monitor survival by counting the number of germlings in five haphazardly chosen 1cm$^2$ areas on each plate. To minimize possible edge effects, a 1cm margin around the edge of each plate was excluded. Size data were collected by measuring 10 random germlings per plate. Due to logistical constraints, germlings for each experiment were not the same age at the start of the experiments, being 3-13 days old (Table 4.1). Percent covers of sediment and ephemeral algae on plates were also recorded.

Experiments were carried out twice for each species to obtain seasonal comparisons. Due to differences in reproductive periodicities it was not always possible to perform experiments at the same time or during the same seasons. Experiments using *H. banksii* were started in the austral summer and winter, and *D. antarctica* in the austral winter and early spring (Table 4.1). Experiments using *F. gardneri* were started in the boreal summer and autumn, and *P. limitata* in the boreal spring and autumn (Table 4.1). The autumn experiments using *F. gardneri* and *P. limitata* were run at the same time.

Survival and growth data were analysed using a general linear model analysis of variance (ANOVA). Sites were treated as random. Homogeneity of variances was checked using Cochran's test, and data were transformed as necessary. If variances could not be stabilised, more conservative p-values were used. Post-hoc comparisons were made using Tukey's tests. Statistica 7 (Copyright© StatSoft Inc.) was used in all analyses.

**Table 4.1.** Starting dates, average settlement densities, and germling ages and sizes for experiments with each species.

| | Species | Spring | Summer | Autumn | Winter |
|---|---|---|---|---|---|
| New Zealand | *Hormosira banksii* | | 2 Dec. 2003<br>300 cm$^{-2}$<br>4 d (57$\mu$m) | 5 May 2004<br>334 cm$^{-2}$<br>3 d (70$\mu$m) | |
| | *Durvillaea antarctica* | 21 Aug.2001<br>1261 cm$^{-2}$<br>13 d (175$\mu$m) | | | 5 Jul. 2003<br>1845 cm$^{-2}$<br>3 d (84$\mu$m) |
| Oregon, U.S.A. | *Fucus gardneri* | | 28 Jun. 2001<br>33 cm$^{-2}$<br>7 d (83$\mu$m) | 9 Oct. 2002<br>178 cm$^{-2}$<br>5 d (97$\mu$m) | |
| | *Pelvetiopsis limitata* | 14 May 2002<br>16 cm$^{-2}$<br>2 d (105$\mu$m) | | 9 Oct. 2002<br>18 cm$^{-2}$<br>5 d (134$\mu$m) | |

### 4.2.3 Settlement methods

Reproductive adult plants were collected and cold-shocked in a refrigerator for 1 - 3 days, and then placed into a warm area for 1 - 2 hours to stimulate gamete release. Gametes were washed from plants and left in buckets for approximately 30 minutes for fertilisation to occur. The zygote suspension was passed through a 100$\mu$m filter to remove debris, and then poured over the artificial plates in a tank with approximately 5cm of seawater covering them. Settlement densities for each species reflected natural settlement densities observed in the

field, but could not always be replicated within species for the seasonal comparisons due to variation in gamete production. Table 4.1 shows the average settlement densities for each species. Plates were left for approximately 24 hours for attachment to occur, after which they were ready for initial monitoring. Prior to this, plates were vigorously washed in running seawater to remove loosely attached germlings that might be removed by initial contact with waves in the field. Settled plates were kept in running seawater until transplantation. Germlings were not constantly submerged prior to outplanting because they were subjected to several emersion times when water was drained from the tanks for short periods and during initial monitorings. Care was taken to keep plates damp and cool during these periods.

## 4.3 Results

### 4.3.1 Community structure

Appendix I contains percent covers of sessile invertebrates, bare space and algae, and numbers of mobile invertebrates across shore heights for sheltered and intermediate habitats at New Zealand and Oregon sites. A striking difference between New Zealand and Oregon sites was that Oregon sites had many perennial and ephemeral algal species in the high shore, and had mid shores dominated by mussels and barnacles. In contrast, New Zealand high and mid shores were dominated by bare space, and mussels were rare (Appendix I: Fig. 1: A, B, E, F; Tables 1 and 2). In addition, Oregon had very high numbers of limpets and littorines (Appendix I: Fig. 3: F, G), with averages of 288, 240 and 175 grazers per $0.25m^2$, compared to averages of 149, 74 and 44 grazers per $0.25m^2$ in the high, mid and low shores in New Zealand (sites combined, Fig. 4.4). However, grazers were very small in Oregon, with only littorines and small limpets (~10-15mm diameter) of the genus *Lottia* present. Although New Zealand had lower numbers of grazers, they were in general much larger (up to 50mm in length), and there was a more diverse range of species including limpets, turbinids, trochids, and chitons (Appendix I, Tables 1 and 2).

In New Zealand, low shores of both exposed sites were dominated by *D. antarctica* with an understorey of coralline algae. In more sheltered situations, coralline algae, *Carpophyllum maschalocarpum, Cystophora* spp., *H. banksii* and encrusting brown algae were abundant. The limpets *Siphonaria australis* and *Patelloida corticata* were the most abundant grazers in the low shore. Mid and high shores were predominately bare rock, with the mid shore having patches of coralline algae and *H. banksii* (Appendix I, Tables 1 and 2). *S. australis* and several other limpet species of *Cellana* were common on the mid and high shores, and littorines (*Austrolittorina antipodum* and *Austrolittorina cincta*) were abundant in the high shore (Appendix I, Fig. 2, B, E; Tables 1 and 2).

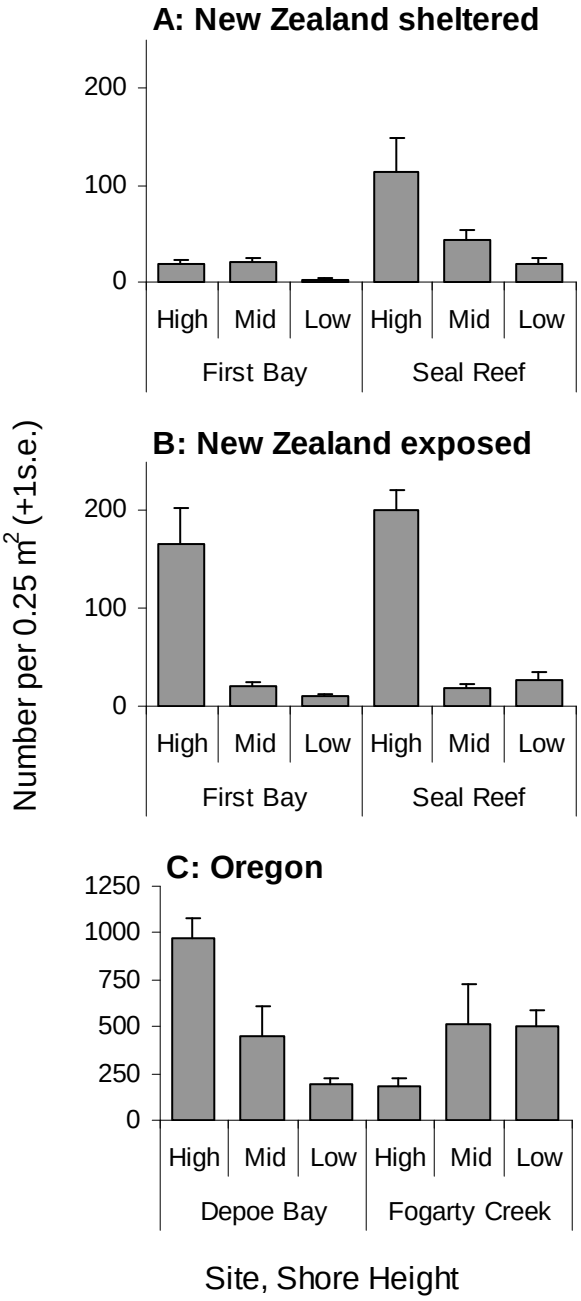


**Figure 4.4** Numbers of total grazers per 0.25 $m^2$ in A: New Zealand sheltered sites, B: New Zealand exposed sites, and C: Oregon sites. $n = 5$. See Appendix I for details of species. Note differences in scale of y-axis.

In Oregon, the low shore at Depoe Bay was dominated by red algae (mainly corallines and *Polysiphonia* sp.) and sessile invertebrates. Limpets (*Lottia* spp.) were very abundant with an average of 196 per 0.25 $m^2$. The Fogarty Creek low shore was dominated by the red alga *Neorhodomela larix* and sessile invertebrates (Appendix I, Table 3). Littorines and limpets were abundant, with averages of 322 and 181 per 0.25 $m^2$ respectively. The mid shores of both sites were dominated by mussels (*Mytilus edulis*), barnacles, littorines and limpets (Appendix I, Table 3; Fig. 3). The high shore at Depoe Bay had mostly bare rock, *P. limitata* and barnacles, and small amounts of *F. gardneri*, *Endocladia muricata* and *Mastocarpus*

*papillatus* (Appendix I, Table 3). Limpets and high numbers of littorines (average of 900 per 0.25 $m^2$) were present. The high shore at Fogarty Creek was dominated by *F. gardneri*, barnacles and mussels, and had a mixture of several other species of algae (*Pelvetiopsis limitata*, *Mazzaella parksii*, *M. papillatus* and *E. muricata* and *Odonthalia floccosa*) (Appendix I; Table 3). Littorines and limpets were also abundant, but at lower abundances than at Depoe Bay (106 and 73 per 0.25 $m^2$ respectively).

### 4.3.2 Physical conditions

*Emersion times*

Maximum, average and total emersion times for the first 14 days of experiments were variable between seasons within the same sites (Table 4.2), and this was more pronounced at Oregon sites. For example, the high shore at Depoe Bay during the *F.gardneri, P.limitata* autumn experiment had maximum, average and total emersion times of 12.5, 7 and 193 hours respectively, whilst during the *P. limitata* spring experiment it had maximum, average and total emersion times of 9.5, 5.3 and 152.5 hours respectively. Oregon sites usually had higher maximum emersion times in high and mid shores than New Zealand sites, but average times were similar.

**Table 4.2** Maximum, average and total emersion times (in hours) in High, Mid and Low zones at each site for the first 14 days of each experiment. Missing data were due to loss of temperature loggers. FB = First Bay, SR = Seal Reef, DB = Depoe Bay and FC = Fogarty Creek. Data marked with * and ** used data from loggers in fence treatments, from the first 4 and 7 days respectively.

| | | Maximum | | | Average | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Experiment | Site | High | Mid | Low | High | Mid | Low | High | Mid | Low |
| *H. banksii* summer | FB | 9.5 | 6** | 6.5 | 7 | 4.6** | 3.2 | 192 | | 90 |
| | SR | 9.5* | 7 | 5.5 | 6.1* | 5.2 | 2.4 | | 147 | 68.5 |
| *H. banksii* autumn | FB | 8.5 | 7.5 | 6.5 | 6.3 | 4.6 | 2.3 | 185 | 133 | 67.5 |
| | SR | 9 | 7 | 6.5 | 7.5 | 5.2 | 2.7 | 201.5 | 140 | 74 |
| *D. antarctica* spring | FB | 9.5 | 7.5 | 5 | 6.7 | 4.9 | 2.7 | 180 | 131 | 74 |
| | SR | 8.5 | | 6 | 6.3 | | 2.7 | 168.5 | | 72 |
| *D. antarctica* winter | FB | 8.5 | 5.5 | 4.5 | 6.7 | 4.4 | 2.8 | 179 | 118 | 77 |
| | SR | 9.5 | 6 | 3.5 | 6.4 | 4.6 | 2.4 | 171.5 | 122 | 63.5 |
| *F.gardneri/P.limitata* | DB | 12.5 | | 6.5 | 7 | | 2.3 | 193 | | 64.5 |
| autumn | FC | 10.5 | 8 | 6.5 | 6.1 | 4.2 | 1.9 | 170 | 116 | 56 |
| *P. limitata* spring | DB | 9.5 | | 6.5 | 5.3 | | 2.6 | 152.5 | | 76.5 |
| | FC | 10 | 8 | 6.5 | 6 | 4.2 | 3 | 167 | 123 | 86 |

*Temperature*

Raw temperature data (Fig. 4.5; Fig 4.6), and maximum and average temperatures (Table 4.3) across shore heights for each site showed that high shores usually had similar temperatures to mid shores, and that low shore temperatures were much lower. The high shore usually had higher temperatures than the mid shore, but occasionally the mid shore had higher maximum

and/or average temperatures (e.g. *D. antarctica* spring experiment at First Bay, Table 4.3; Figure 4.5 C). Comparisons of temperatures between experiments showed highly variable temperatures between seasons and sites. As expected, experiments during warmer months had higher maximum and average temperatures, and more frequent temperature spikes. Temperatures in autumn and winter experiments were usually at sea temperature or cooler, but did have some periods when they exceeded 20˚C. For example, the *H. banksii* autumn experiment at Seal Reef (Figure 4.5, B) and the *F. gardneri, P. limitata* autumn experiment at Depoe Bay and Fogarty Creek (Figure 4.6, B) had temperature spikes in days 1-4. During some experiments, temperatures were highly variable between sites. For example, Seal Reef experienced much higher emersion temperatures than First Bay during days 1-4 of the *H. banksii* autumn experiment (Figure 4.5 B).

**Table 4.3** Maximum and average emersion temperatures (˚C) during the first 14 days, across shore heights for each site and each experiment. FB = First Bay, SR = Seal Reef, DB = Depoe Bay and FC = Fogarty Creek.

| | | Maximum | | | Average | | |
|---|---|---|---|---|---|---|---|
| Species, season | Site | High | Mid | Low | High | Mid | Low |
| *H. banksii* summer | FB | 44.5 | 30.5 | 24.5 | 19.0 | 16.7 | 15.7 |
| | SR | 37 | 36.5 | 35 | 18.7 | 18.4 | 16.8 |
| *H. banksii* autumn | FB | 15 | 15 | 13.5 | 9.9 | 10.9 | 11.4 |
| | SR | 27 | 26.5 | 22.5 | 11.5 | 12.1 | 11.9 |
| *D. antarctica* spring | FB | 25 | 29 | 12.9 | 10.6 | 10.7 | 9.5 |
| | SR | 24.7 | | 11.8 | 10.2 | | 9.8 |
| *D. antarctica* winter | FB | 16.5 | 19.5 | 17.5 | 6.8 | 7.2 | 7.6 |
| | SR | 20.5 | 22.5 | 14 | 6.8 | 7.1 | 8.6 |
| *F.gardneri* summer | DB | | 23.7 | | | 13.2 | |
| | FC | | 22.5 | | | 11.9 | |
| *F.gardneri, P.limitata* autumn | DB | 34.5 | | 32.5 | 10.6 | | 10.5 |
| | FC | 27 | 12 | 12.5 | 8.5 | 7.8 | 6.3 |
| *P. limitata* spring | DB | 38.5 | | 34 | 16.1 | | 15.7 |
| | FC | 33.5 | 32 | 33.5 | 15.1 | 10.3 | 16 |

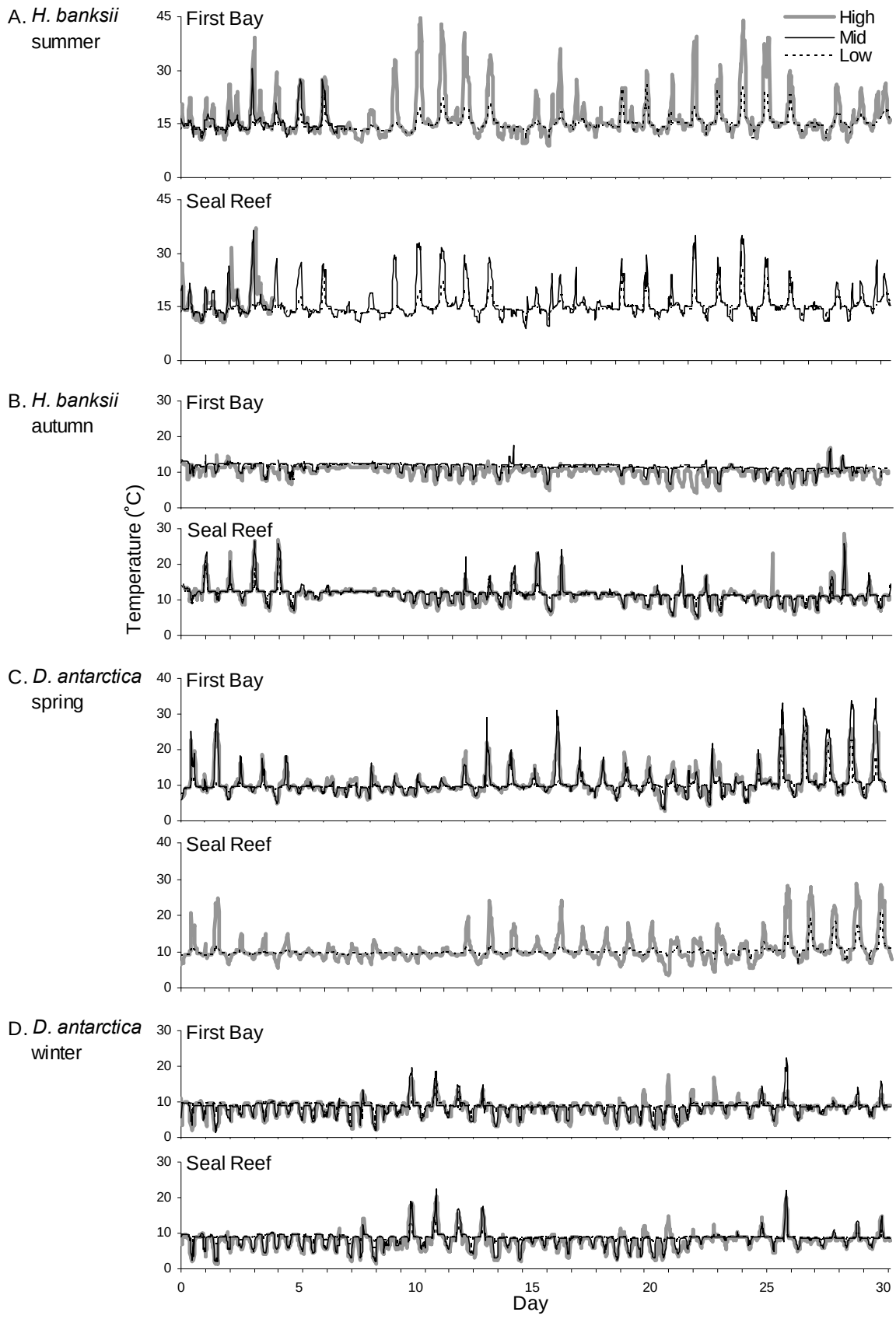


**Figure 4.5** Kaikoura temperatures for days 1-30 in high, mid and low shores at each site. A. *H. banksii* summer; B. *H. banksii* autumn; C. *D. antarctica* spring; and D. *D. antarctica* winter.

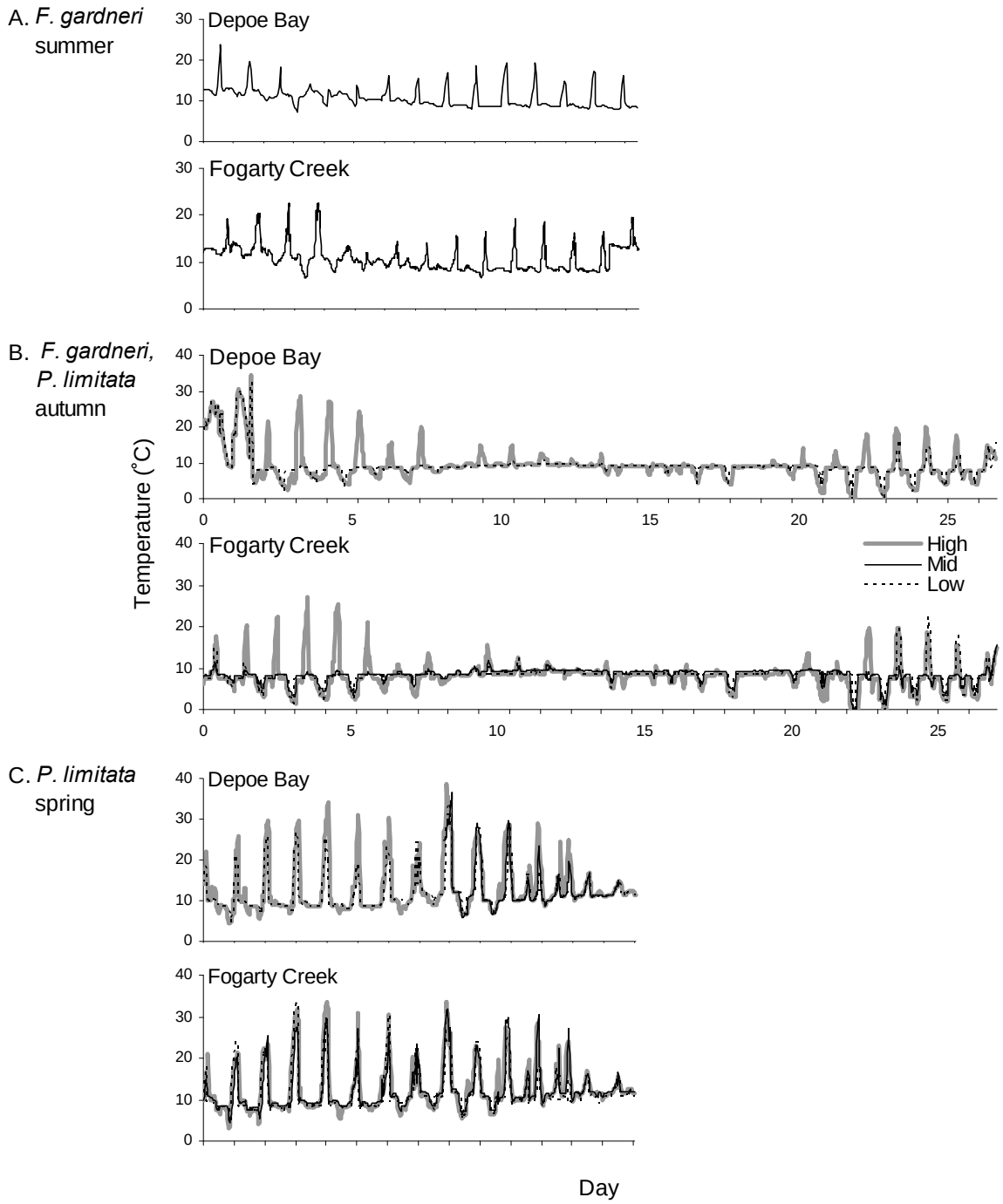


**Figure 4.6** Oregon temperatures for days 1-14 or 1-26 in high, mid and low shores at each site. A. *F. gardneri* summer; B. *F. gardneri*, *P. limitata* autumn; C. *P. limitata* spring. Temperature was recorded only in the mid shore in the *F. gardneri* summer experiment.

Comparison of emersion temperatures from fence and fence + shade treatments showed that shade had variable effects on temperature (Table 4.4**)**. In general, during cool temperatures, shade slightly increased temperatures and during intense temperature spikes, shade decreased temperatures. For example, a fence + shade treatment in the mid shore in the *D. antarctica* winter experiment had a maximum temperature 1˚C higher than the fence treatment, and a fence + shade treatment in the mid shore in the *H. banksii* summer experiment had a maximum temperature 5˚C lower than the fence treatment (Table 4.4).

**Table 4.4** Differences in average and maximum emersion temperatures between fence+shade and fence treatments, sites combined. Data for New Zealand *H. banksii* and *D. antarctica* experiments are from days 1-7, and data for Oregon *P. limitata* experiment are from days 8 - 14.

| | *H. banksii* | | | | *D. antarctica* | | *P. limitata* | |
|---|---|---|---|---|---|---|---|---|
| | Summer | | Autumn | | Winter | | Spring | |
| Shore Height | Ave. | Max. | Ave. | Max. | Ave. | Max. | Ave. | Max. |
| High | | | -0.2 | -1.5 | 0.6 | 0.5 | | |
| Mid | -1.3 | -5.0 | 0.8 | -1.0 | 0.2 | 1.0 | -1.15 | -7.5 |
| Low | -0.9 | -7.3 | -0.7 | -1.0 | 0.2 | 0.0 | | |

*Wave climate*

Average dynamometer readings in the low shore during each experiment (sites combined) are shown in Fig. 4.7. Most experiments had fairly similar wave climates, except for *H. banksii* autumn and *D. antarctica* spring, which had lower and higher average maximum wave forces respectively.

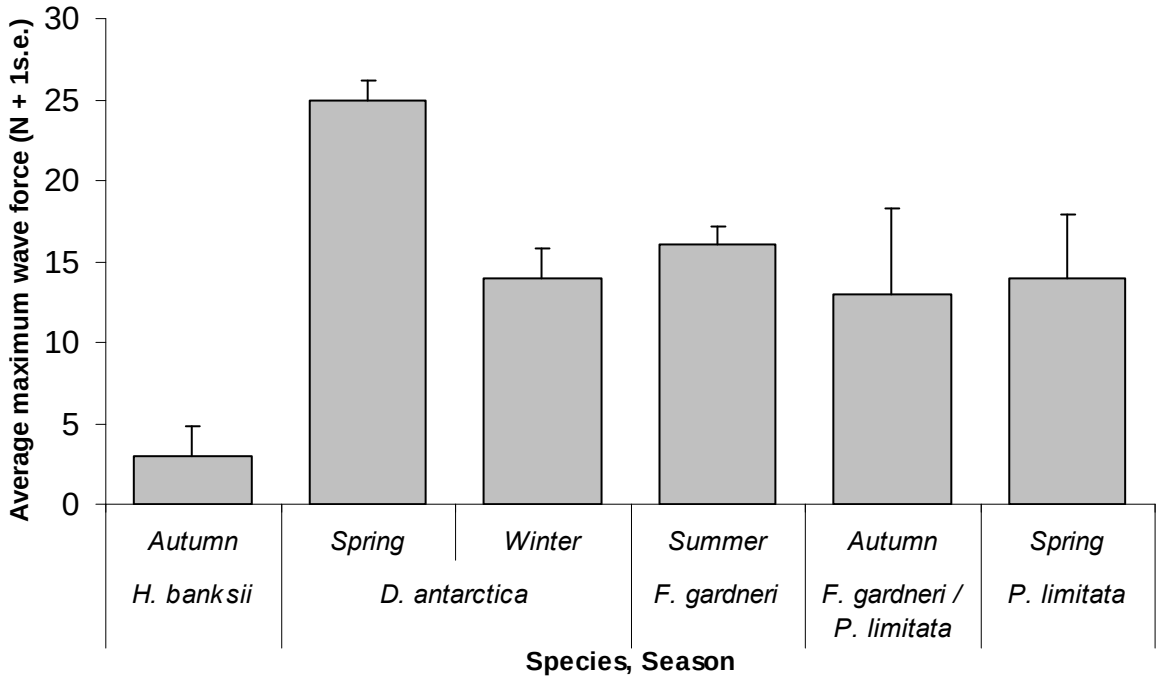


**Figure 4.7** Average maximum wave forces in the low shore during each experiment (data was not collected during the *H. banksii* summer experiment).

### 4.3.3 Survival and growth within species

#### *Hormosira banksii* - summer

After 1 day in summer, survival had declined to between 42-76% but was not significantly different between sites, shore heights or treatments (Fig. 4.8, Table 4.5). At subsequent times germling survival was significantly influenced by shore height, and there was a significant shore height x treatment, or site x shore height x treatment interaction effect. Regardless of site or treatment, high shore germlings had very poor survival with 100% mortality within 4 days. Mid shore germlings had slightly better survival, but all germlings without shade had died by Day 7. Shade increased survival temporarily in the mid shore, and germlings at First Bay had higher survival on Days 7 and 13 than those at Seal Reef. All mid shore germlings had died by Day 32. The low shore had greater survival, with 39% and 65% of fenced germlings surviving after 32 days at First Bay and Seal Reef respectively. Shade had different effects on survival at each site, increasing survival at First Bay (39% vs. 53% survival at Day 32 on low shore fence and fence + shade treatments respectively), and decreasing survival at Seal Reef (65% vs. 30% survival at Day 32 on fence and fence + shade treatments respectively). Fencing plates from grazers enhanced survival at both sites.

Maximum temperatures showed spikes in the high and mid shores on Day 3, with maxima of 39°C and 36°C respectively (Fig. 4.8). The low shore maximum temperature on Day 3 was only 19.5°C. The low shore did experience high temperatures later in the experiment, and temperatures were much higher at Seal Reef than at First Bay. Maximum temperatures in the low shore for the duration of the experiment were 39°C and 26°C at Seal Reef and First Bay respectively.

The death of high and mid shore germlings made full comparisons of sizes across shore heights impossible. Sizes were significantly different between shore heights in the mid and low shore shaded treatments on Day 13 ($F_{1,8}$=909.8668; $p$<0.001), with larger germlings in the low shore (Fig. 4.9). Comparison of sizes in the fence and fence+shade treatments in the low shore showed no treatment effects on all monitor days.

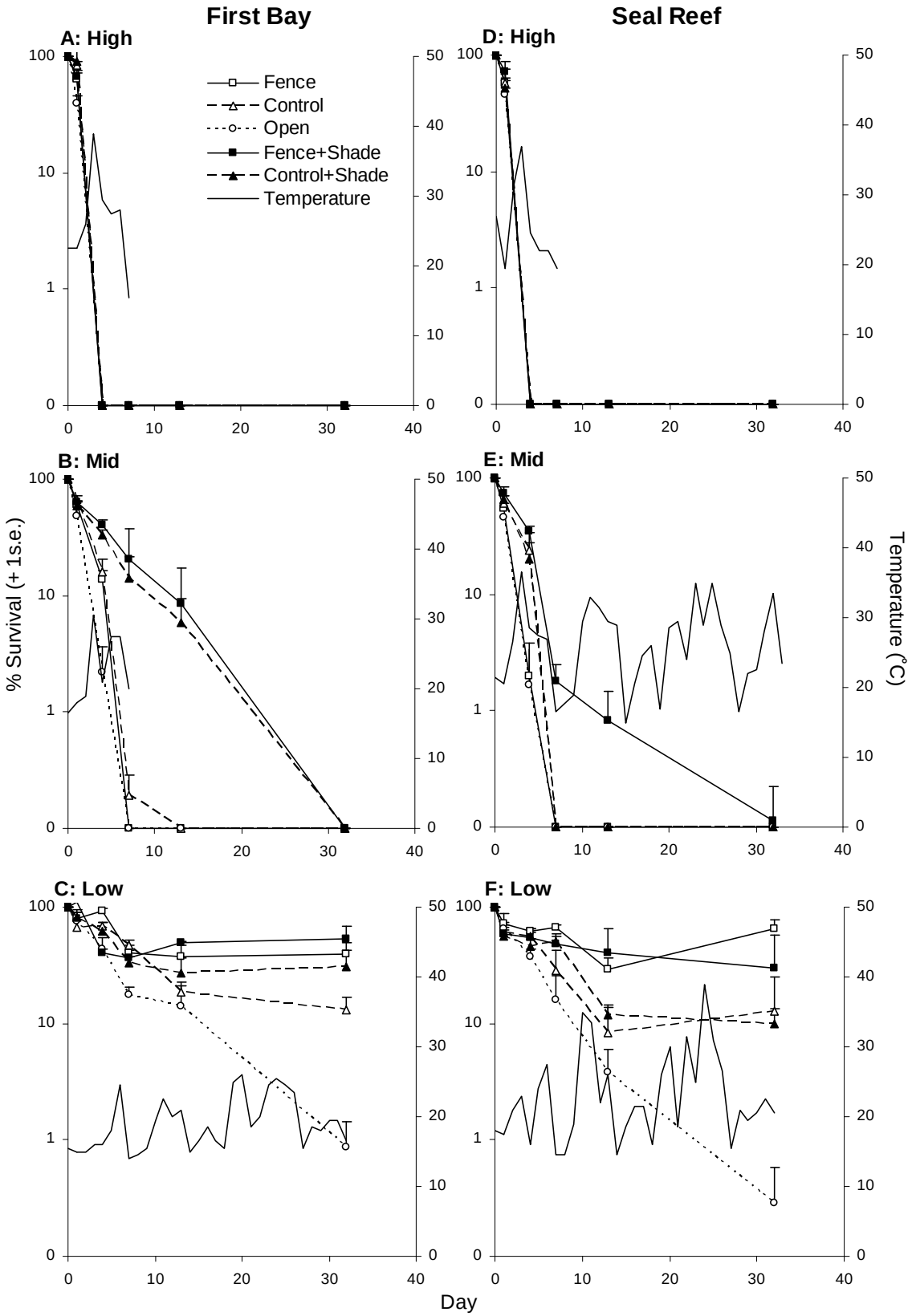


**Figure 4.8** Summer 2003, Kaikoura. Percent survival of *H. banksii* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at First Bay (A-C) and Seal Reef (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis.

**Table 4.5** ANOVA results of *H. banksii* survival across sites, shore heights, grazing and heat stress/desiccation treatments in summer 2003. Sites were treated as random. Cochran's test was significant on Day 32, and data were square root transformed to stabilize variances. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

| | | Day 1 | | Day 4 | | Day 7 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 2373.9 | 4.421 | 537.40 | 2.164 | 0.51 | 0.00 |
| Shore Height (SH) | 2 | 1366.2 | 1.564 | **24659.29** | **127.704**** | **13576.89** | **38.96*** |
| Treatment (TMT) | 4 | 1003.9 | 5.557 | 659.37 | 3.295 | 488.44 | 3.50 |
| Site*SH | 2 | 873.6 | 1.689 | 193.10 | 1.333 | 348.49 | 1.54 |
| Site*TMT | 4 | 180.7 | 0.349 | 200.10 | 1.382 | 139.51 | 0.62 |
| SH*TMT | 8 | 329.1 | 0.636 | **870.27** | **6.009*** | 384.91 | 1.70 |
| Site*SH*TMT | 8 | 517.3 | 1.259 | 144.84 | 1.780 | **225.79** | **2.49*** |
| Error | 60 | 410.8 | | 81.37 | | 90.83 | |

| | | Day 13 | | Day 32 | |
|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* |
| Site | 1 | 445.82 | 1.901 | 2.62 | 62.996 |
| Shore Height (SH) | 2 | **5375.13** | **23.482*** | **162.62** | **0.948*** |
| Treatment (TMT) | 4 | **526.70** | **36.580**** | **12.56** | **55.542*** |
| Site*SH | 2 | **228.91** | **25.916***** | 2.93 | 7.052 |
| Site*TMT | 4 | 14.40 | 1.630 | 1.78 | 1.504 |
| SH*TMT | 8 | **399.60** | **45.240***** | **12.36** | **0.915**** |
| Site*SH*TMT | 8 | 8.83 | 0.082 | 1.95 | 6.348 |
| Error | 60 | 108.29 | | 1.59 | 1.226 |

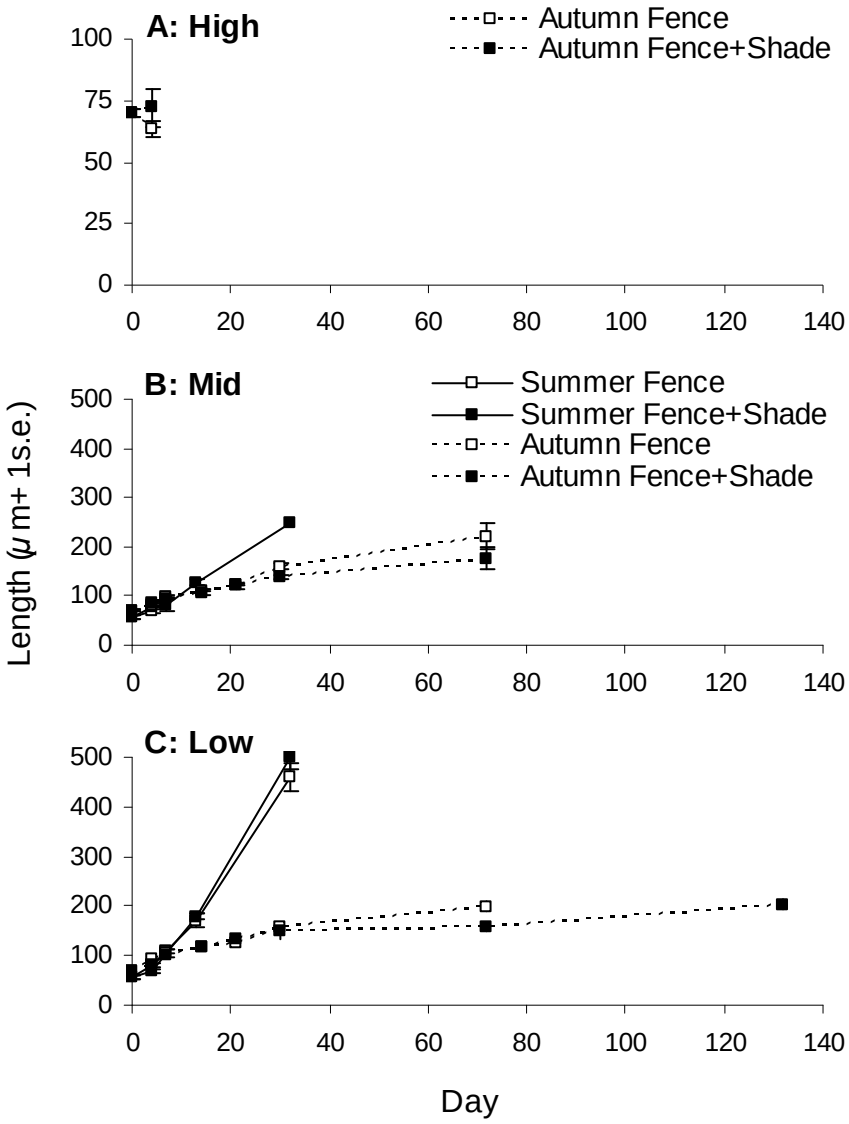


**Figure 4.9** Average lengths of *H. banksii* germlings transplanted upshore (A: High shore, B: Mid shore, C: Low shore) in Fence and Fence+Shade treatments in summer 2003 (solid lines) and autumn 2004 (dashed lines). Note differences in scale of y-axis.

***Hormosira banksii* - autumn**

Survival of germlings in autumn was significantly influenced by treatment and there were significant site x shore height and shore height x treatment interactions (Fig. 4.10; Table 4.6). As in summer, all high shore germlings had died by Day 4. However, mid shore germlings had much better survival. At Day 30 survival in mid shore fenced treatments was 66% and 22% at First Bay and Seal Reef respectively. Survival in the low shore was similar to summer, with 68% and 31% survival in fenced treatments on Day 30 at First Bay and Seal Reef respectively. Mid and low shore plates open to grazing had less than 5% survival by Day 30.

Seal Reef experienced much higher maximum temperatures than First Bay (Table 4.3; Fig. 4.5; Fig. 4.10). For example, maximum temperatures by Day 4 were only 12-15°C at

First Bay, but were 21-26.5°C at Seal Reef. However, temperatures were much lower than during summer.

Sizes were significantly different between shore heights within 4 days ($F_{2,20}$ = 10.561, $p$<0.001). There was also a significant shore height x treatment interaction effect on Day 4 ($F_{2,20}$ = 191.7, $p$<0.05) due to shade-enhanced growth in the high and mid shore, but decreased growth in the low shore (Fig. 4.9). Germlings were longer in the mid and low shore fence+shade treatments (Tukey HSD $p$<0.05) and low shore fence treatments (Tukey HSD $p$<0.01), than the high shore fenced treatments. Germlings in the low shore fenced treatments were also significantly longer than the high shore fence+shade treatments (Tukey HSD $p$<0.05). Subsequent analyses could only use data from the mid and low shore because all high shore germlings had died. There were no significant differences in sizes between the mid and low shores or between treatments on Days 8, 21 and 30. There were significant differences between the mid and low shores on Day 14 ($F_{1,17}$ = 4.755, $p$<0.05), with larger germlings on the low shore. There was a significant treatment effect on Day 72 ($F_{1,16}$ = 7.6139, $p$<0.05), with larger germlings in the mid shore fenced treatments compared to the low shore fenced+shade germlings (Tukey HSD $p$<0.05).

There was a significant season x shore height interaction effect on survival of fenced treatments at Day 14 ($F_{2,30}$ = 6.177035, $p$<0.01). The high shores had 0% survival, but the mid and low shores had higher survival in autumn than in summer (Tukey HSD mid autumn vs. mid summer $p$< 0.01; low autumn vs. low summer $p$<0.01).

There was a significant effect of season on germling growth (Day 14 growth of low shore fenced treatments, $F_{1,10}$ = 21.1200, $p$<0.001). Growth in autumn was much slower than that in summer, with low shore fenced germlings having grown on average only 88 μm at Day 14 and 131 μm after Day 30 (c.f. 114 μm and 404 μm growth for low shore fenced germlings after Day 13 and Day 32 respectively in summer) (Fig. 4.9). During autumn, after 72 days the average sizes of fenced and fenced + shaded germlings in the mid and low shores were only 220 and 200 μm, and 176 and 156 μm respectively, and after 132 days the fenced + shaded germlings were only around 200 μm.

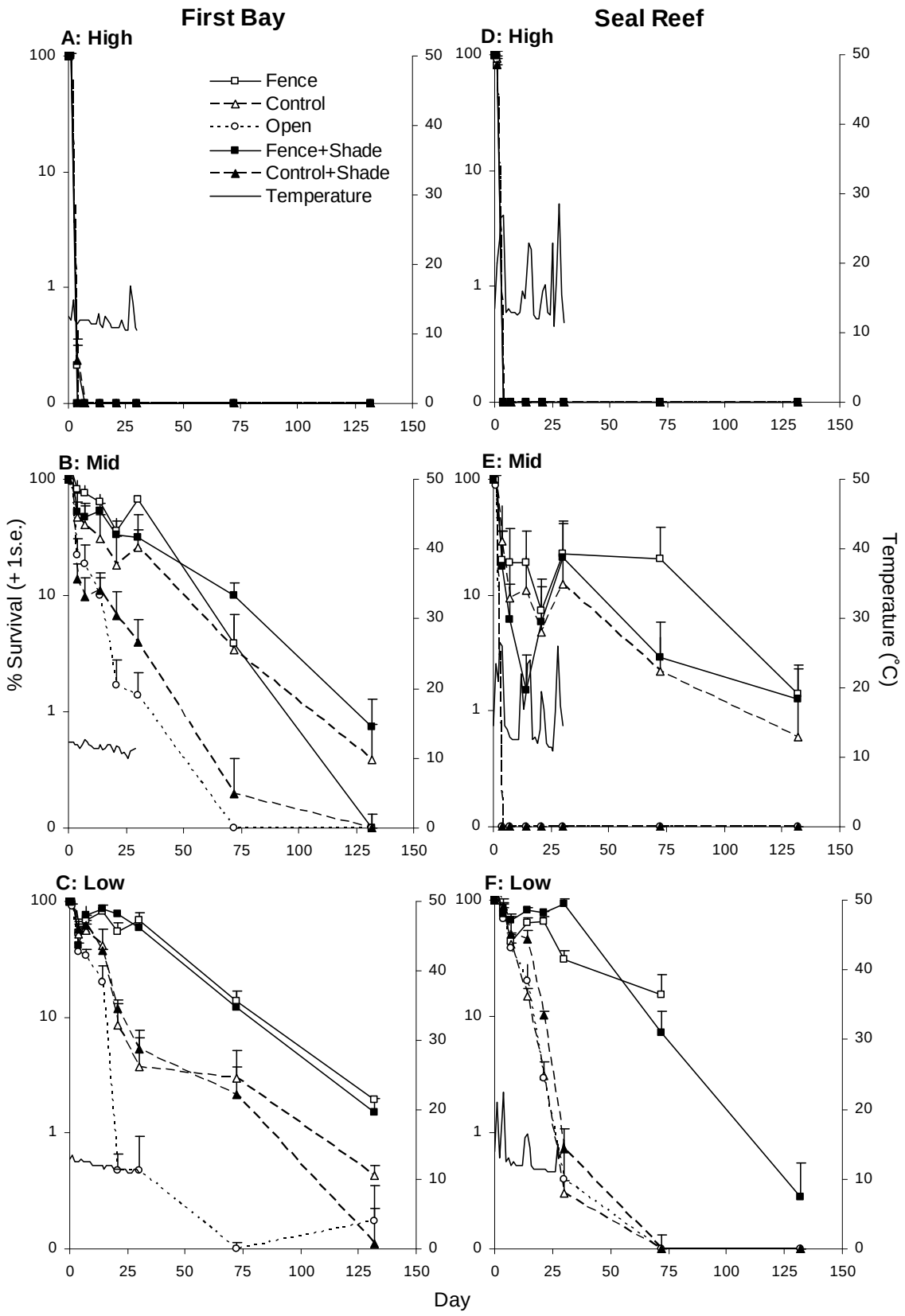


**Figure 4.10** Autumn 2004, Kaikoura. Percent survival of *H. banksii* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at First Bay (A-C) and Seal Reef (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis.

**Table 4.6** ANOVA results of *H. banksii* survival across sites, shore heights, grazing and heat stress/desiccation treatments in autumn 2004. Sites were treated as random. Cochran's tests were significant on days 4, 21 and 30, and data were square root transformed to stabilize variances. Day 30 data could not be stabilized, but square root transformed data gave more conservative p-values. * $P$<0.05, ** $P$<0.01, *** $P$<0.001.

| | | Day 1 | | Day 4 | | Day 7 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 2104 | 3.051 | 11.90 | 0.166 | 4499.47 | 2.133 |
| Shore Height (SH) | 2 | 2334 | 4.174 | 454.77 | 6.369 | 21861.34 | 11.456 |
| Treatment (TMT) | 4 | **2153** | **6.854*** | **8.80** | **10.144*** | 1205.01 | 3.391 |
| Site*SH | 2 | 559 | 3.043 | **71.40** | **115.778***** | **1908.30** | **12.356**** |
| Site*TMT | 4 | 314 | 1.709 | 0.87 | 1.406 | 355.40 | 2.301 |
| SH*TMT | 8 | 494 | 2.690 | 7.34 | **11.901**** | **744.12** | **4.818*** |
| Site*SH*TMT | 8 | 184 | 0.275 | 0.62 | 0.168 | 154.44 | 0.738 |
| Error | 60 | 669 | | 3.67 | | 209.36 | |

| | | Day 14 | | Day 21 | | Day 30 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 3074.76 | 1.896 | 16.63 | 0.884 | 23.35 | 1.804 |
| Shore Height (SH) | 2 | 18436.32 | 12.284 | 161.80 | 8.582 | 111.47 | 9.604 |
| Treatment (TMT) | 4 | **3285.16** | **8.981*** | **45.03** | **38.415**** | **65.67** | **18.438**** |
| Site*SH | 2 | **1500.83** | **6.120*** | **18.85** | **15.627**** | **11.61** | **5.222*** |
| Site*TMT | 4 | 365.77 | 1.491 | 1.17 | 0.972 | 3.56 | 1.603 |
| SH*TMT | 8 | **1380.57** | **5.629*** | **18.63** | **15.442***** | **24.29** | **10.928**** |
| Site*SH*TMT | 8 | 245.25 | 1.531 | 1.21 | 0.894 | 2.22 | 0.828 |
| Error | 60 | 160.14 | | 1.35 | | 2.69 | |

***Durvillaea antarctica* – Spring**

There were significant treatment, site x shore height, shore height x treatment and site x shore height x treatment interaction effects on survival of *D. antarctica* germlings during spring (Fig. 4.11; Table 4.7). On Day 7 high shore fenced treatments had 7 % and 1% survival at First Bay and Seal Reef respectively, and nearly all germlings in the high and mid shore open treatments had died. Shade enhanced survival, with 40% and 21% survival in high shore fence+shade treatments at First Bay and Seal Reef respectively. Survival was similar across all shore heights in the fence+shade treatments. Across all treatments, mid and low shore germlings had higher survival than those in the high shore. There was less of a treatment effect in the low shore at both sites compared with the high and mid shores.

The high and mid shores experienced much higher maximum temperatures than the low shores in the first 25 days (Fig. 4.5; Fig. 4.11), with maximums of 25°C, 31°C and 13°C in the high, mid and low shores respectively.

Sizes on Day 14 showed significant differences between shore heights ($F_{2,23}$= 6.4245, $p$<0.01) and treatments ($F_{1,23}$=11.8844, $p$<0.01) (Figure 4.12). The mid and low shore fence+shade and low shore fence treatments were significantly longer than the high shore

fence treatments (Tukey HSD mid fence+shade vs. high fence $p<0.01$; Tukey HSD low fence and fence+shade vs. high fence $p< 0.05$). In general, germlings were largest in the low shore, and smallest in the high shore. The exception to this was that the fence+shade germlings on the mid shore were larger than those on the low shore. Shade enhanced growth in the high and mid shores, but had no effect on the low shore.

**Table 4.7** ANOVA results of *D. antarctica* survival across sites, shore heights, grazing and heat stress/desiccation treatments in spring 2001. Sites were treated as random. Cochran's tests were significant, and data were square root transformed to stabilize variances. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

| | | Day 1 | | Day 7 | | Day 14 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 33.096 | 5.1301 | 9.1446 | 1.22687 | 9.7526 | 2.63507 |
| Shore Height (SH) | 2 | 14.541 | 2.5684 | 19.5889 | 2.72105 | 17.4823 | 2.97959 |
| Treatment (TMT) | 4 | 0.580 | 0.0540 | **32.6527** | **20.47904**** | **41.2506** | **27.46690**** |
| Site*SH | 2 | 5.661 | 0.5691 | **7.1990** | **5.44885*** | 5.8673 | 1.61244 |
| Site*TMT | 4 | 10.741 | 1.0795 | 1.5944 | 1.20935 | 1.5018 | 0.41419 |
| SH*TMT | 8 | 0.945 | 0.0949 | **5.2967** | **4.04188*** | 7.1265 | 1.95022 |
| Site*SH*TMT | 8 | **9.955** | **2.1569*** | 1.3104 | 0.63427 | 3.6542 | 1.43655 |
| Error | 59 | 4.615 | | 2.0661 | | 2.5437 | |

| | | Day 64 | |
|---|---|---|---|
| Factor | df | MS | *F* |
| Site | 1 | 0.031359 | 0.05967 |
| Shore Height (SH) | 2 | 0.525028 | 0.93779 |
| Treatment (TMT) | 4 | **0.615956** | **22.69676**** |
| Site*SH | 2 | **0.559855** | **9.21452**** |
| Site*TMT | 4 | 0.027139 | 0.44375 |
| SH*TMT | 8 | **0.300586** | **4.89118*** |
| Site*SH*TMT | 8 | 0.061455 | 1.39314 |
| Error | 59 | 0.044112 | |

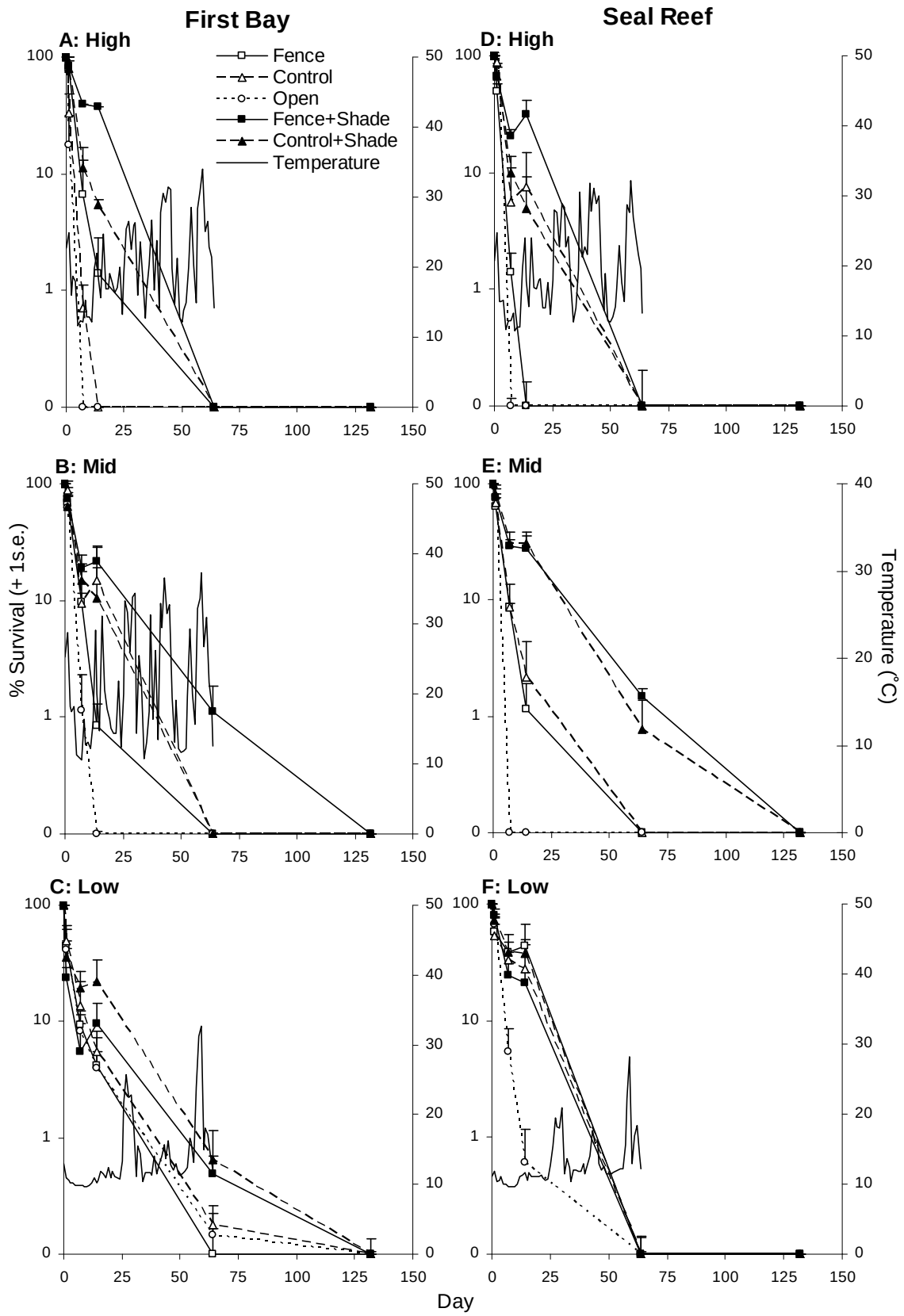


**Figure 4.11** Spring 2001, Kaikoura. Percent survival of *D. antarctica* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at First Bay (A-C) and Seal Reef (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis. Temperature data logger was vandalized and data lost from Seal Reef mid shore.

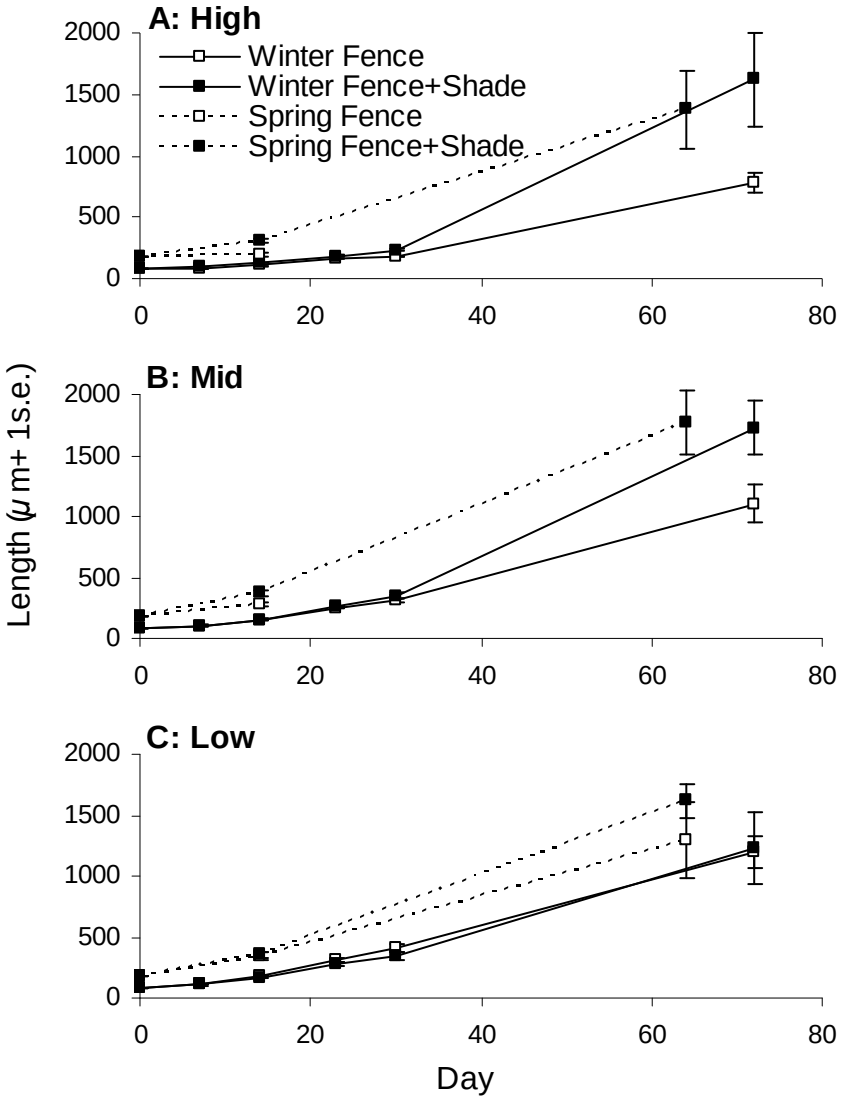


**Figure 4.12** Average lengths of *D. antarctica* germlings transplanted upshore (A: High shore, B: Mid shore, C: Low shore) in Fence and Fence+Shade treatments in spring 2001 (dashed lines) and winter 2003 (solid lines).

***Durvillaea antarctica* – Winter**

Survival was not significantly different between sites, shore heights or treatments until Day 7 in winter (Fig. 4.13; Table 4.8). On Day 7 there were significant treatment and site x shore height interaction effects. In subsequent monitor times there were significant treatment, site x shore height interaction and shore height x treatment interaction effects on Day 14, significant shore height and site x shore height x treatment interaction effects on Day 23, and significant shore height and treatment effects on Day 30. Patterns of survival were similar to the spring experiment. Shade enhanced survival in the high and mid shores at both sites, and in the low shore at Seal Reef. In general, fence controls and open plates had lower survival than other treatments.

The high and mid shores had much lower temperatures than in the spring experiment (c.f. Table 4.3; Fig. 4.5; Fig. 4.13), with maximum temperatures of 20.5°C and 22.5°C in the high and mid shores respectively in the first 30 days. In addition, all shore heights had fewer temperature spikes.

Sizes were significantly different between shore heights on Days 7, 14, 23 and 30 (Day 7: $F_{2,30}$=10.123 $p$<0.001; Day 14: $F_{2,28}$=69.661 $p$<0.0001; Day 23: $F_{2,24}$=46.48 $p$<0.0001; Day 30: $F_{2,26}$=28.23 $p$<0.001;). Low shore germlings were the largest and high shore germlings were the smallest (Fig. 4.12). There were significant shore height x treatment interaction effects on Days 14 and 30 (Day 14: $F_{2,28}$=4.056 $p$<0.05; Day 30: $F_{2,24}$=4.03 $p$<0.0001;. This was due to the treatments acting differently at each shore height. Sometimes shade enhanced growth (for example, in the high shore), and at other times it had negative effects on growth (for example, in the low shore).

There was a significant season x shore height interaction effect on survival of fenced treatments at Day 14 ($F_{2,27}$ = 3.636912, $p$<0.05). Mid shore survival was higher during winter than in spring (Tukey HSD $p$<0.001). Survival was not significantly different in the high and low shores.

Growth was significantly different between seasons (Day 14 fenced treatments: $F_{1,22}$=10.01836 $p$<0.05), with faster growth in spring than winter. After 14 days, spring germlings in fenced treatments had grown on average 104 μm and 170 μm in the mid and low shores respectively, and winter germlings had only grown 70 μm and 98 μm in the mid and low shores respectively. However, these results should be interpreted with caution because spring germlings were 10 days older than winter germlings (Table 4.1).

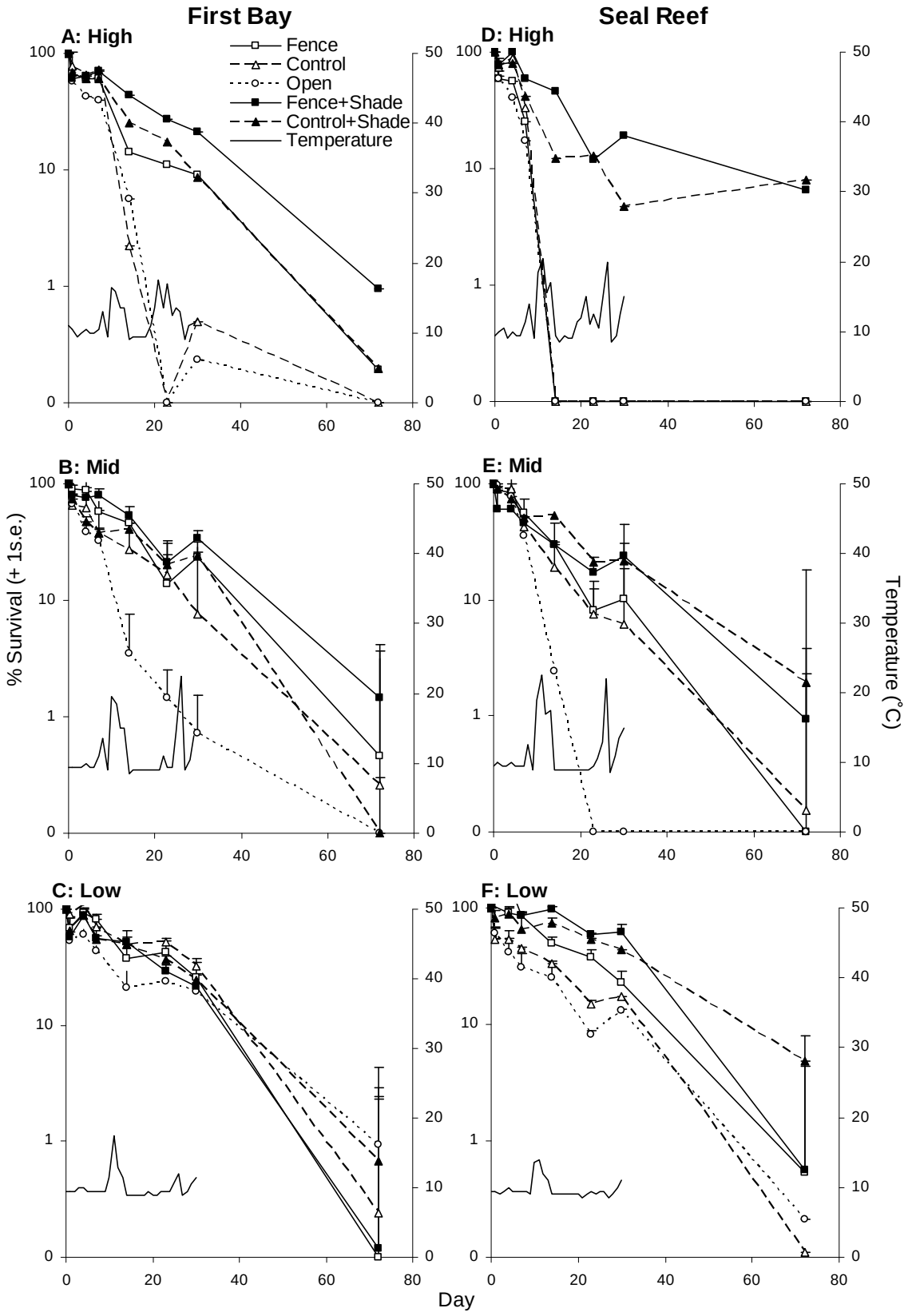


**Figure 4.13** Winter 2003, Kaikoura. Percent survival of *D. antarctica* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at First Bay (A-C) and Seal Reef (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis.

**Table 4.8** ANOVA results of *D. antarctica* survival across sites, shore heights, grazing and heat stress/desiccation treatments in winter 2003. Sites were treated as random. Cochran's tests were non-significant for Day 1, and significant for all other days. Data were square root transformed to stabilize variances; Days 23 and 72 could not be stabilized but square root transformed data gave more conservative p-values. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

| | | Day 1 | | Day 4 | | Day 7 | | Day 14 | |
|---|---|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 2424.9 | | 9.49 | 4.45 | 0.382 | 2.329 | 10.81 | 1.178 |
| Shore Height (SH) | 2 | 1122.5 | 3.260 | 13.68 | 127.94 | 11.134 | 2.409 | 10.15 | 1.055 |
| Treatment (TMT) | 4 | 483.6 | 1.164 | 14.47 | **63.08** | **27.208**** | 3.843 | **13.71** | **9.646*** |
| Site*SH | 2 | 344.4 | 0.292 | 5.68 | **11.49** | **5.329*** | 1.058 | **9.62** | **5.149*** |
| Site*TMT | 4 | 415.4 | 0.352 | 3.77 | 2.32 | 1.075 | 0.701 | 1.42 | 0.761 |
| SH*TMT | 8 | 565.2 | 0.479 | 4.46 | **8.17** | **3.789*** | 0.831 | 1.87 | 1.002 |
| Site*SH*TMT | 8 | 1180.2 | 1.489 | 5.37 | 2.16 | 0.738 | 1.563 | 1.87 | 1.125 |
| Error | 60 | 792.4 | | 3.44 | 2.92 | | | 1.66 | |

| | | Day 23 | | Day 30 | | Day 72 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 14.63 | 4.179 | 7.71 | 2.015 | 2.73 | 1.377 |
| Shore Height (SH) | 2 | **92.34** | **39.345*** | **81.94** | **28.640*** | 0.30 | 0.992 |
| Treatment (TMT) | 4 | 34.53 | 4.581 | **38.45** | **10.320*** | 3.17 | 1.638 |
| Site*SH | 2 | 2.35 | 0.368 | 2.86 | 1.037 | 0.31 | 1.182 |
| Site*TMT | 4 | 7.54 | 1.181 | 3.73 | 1.350 | **1.94** | **7.495**** |
| SH*TMT | 8 | 4.40 | 0.690 | 3.54 | 1.285 | 0.52 | 1.999 |
| Site*SH*TMT | 8 | **6.38** | **2.308*** | 2.76 | 1.334 | 0.26 | 0.513 |
| Error | 60 | 2.77 | | 2.07 | | 0.50 | |

***Fucus gardneri* – Summer**

In summer, there was an overwhelming effect of shade in the high and mid shore, where nearly all germlings without shade had died by Day 4 at Depoe Bay, and Day 8 at Fogarty Creek. Treatment was significant on Days 4, 8 and 14, and site was significant on Days 1, 4, and 14. Survival was never significantly affected by shore height, but interaction terms were significant on Days 1, 4 and 8 (Fig. 4.14; Table 4.9).

Temperatures were only available for the mid shore, and the maximum temperature for the duration of the experiment occurred on the first day (23.7°C at Depoe Bay) (Table 4.3; Fig. 4.6, A,B; Fig. 4.14). Temperatures at the two sites were usually similar, except for Days 3 and 4 when the maximum temperatures at Fogarty Creek were 8°C higher than at Depoe Bay.

Sizes were significantly different between shore heights on Day 4 ($F_{2,26}$=12.449 $p<0.001$) and Day 8 ($F_{2,22}$=5.889 $p<0.01$). By Day 14 all fenced germlings had died in the high and mid shores so only a comparison of the fence+shade treatments across shore heights, and a comparison of the fence and fence+shade treatments in the low shore were possible. On

Day 14 shaded treatments were not significantly different between shore heights. Shade had a positive effect on the low shore ($F_{1,6}$=9.260, p<0.05) (Fig 4.15).

**Table 4.9** ANOVA results of *F. gardneri* survival across sites, shore heights, grazing and heat stress/desiccation treatments in summer 2001. Sites were treated as random. Cochran's tests were non-significant. * *P*<0.05, ***P*<0.01, ****P*<0.001.

| | | Day 1 | | Day 4 | | Day 8 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 920.5 | 2.43 | 6134.1 | 5.59 | 4.72 | 0.005 |
| Shore Height (SH) | 2 | 63.2 | 0.22 | 1816.3 | 3.81 | 88.34 | 0.117 |
| Treatment (TMT) | 4 | 1388.0 | 5.38 | **6977.4** | **8.74*** | **7243.84** | **30.124**** |
| Site*SH | 2 | 288.1 | 1.73 | 476.8 | 2.69 | **752.0** | **16.137**** |
| Site*TMT | 4 | 258.0 | 1.55 | **797.9** | **4.51*** | **240.5** | **5.160*** |
| SH*TMT | 8 | **625.0** | **3.75*** | **778.6** | **4.40*** | **765.2** | **16.419***** |
| Site*SH*TMT | 8 | 166.8 | 1.10 | 176.9 | 1.39 | 46.6 | 0.730 |
| Error | 60 | 152.3 | | 127.7 | | 63.86 | |

| | | Day 14 | |
|---|---|---|---|
| Factor | df | MS | *F* |
| Site | 1 | 237.8 | 2.39 |
| Shore Height (SH) | 2 | 22.0 | 0.15 |
| Treatment (TMT) | 4 | **1089.1** | **18.70**** |
| Site*SH | 2 | 142.5 | 1.41 |
| Site*TMT | 4 | 58.2 | 0.58 |
| SH*TMT | 8 | 62.0 | 0.61 |
| Site*SH*TMT | 8 | 101.2 | 1.91 |
| Error | 60 | 52.9 | |

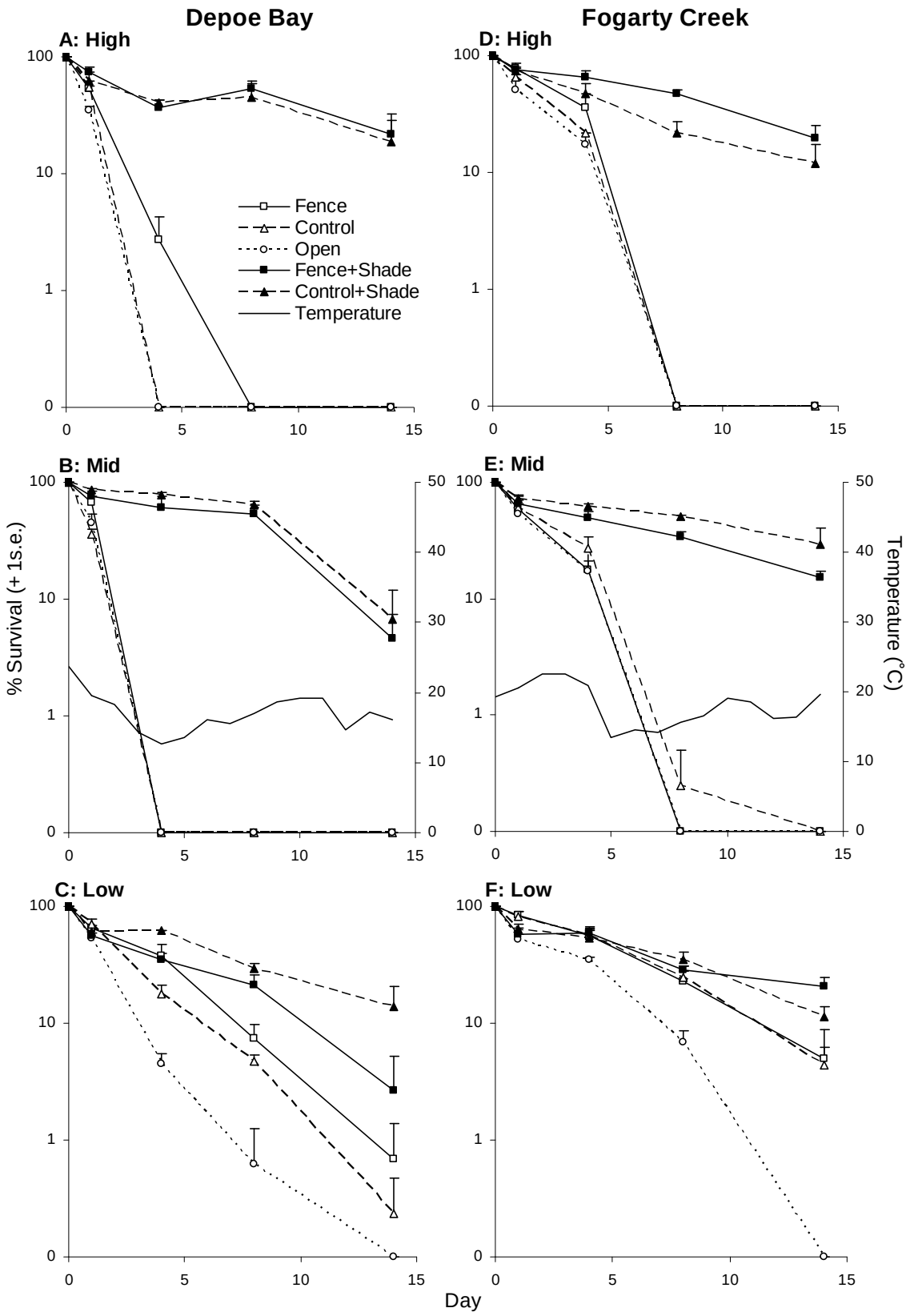


**Figure 4.14** Summer 2001, Oregon. Percent survival of *F. gardneri* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at Depoe Bay (A-C) and Fogarty Creek (D-F). Replicates = 3. Maximum daily temperatures in the mid shore are plotted on a secondary y-axis.

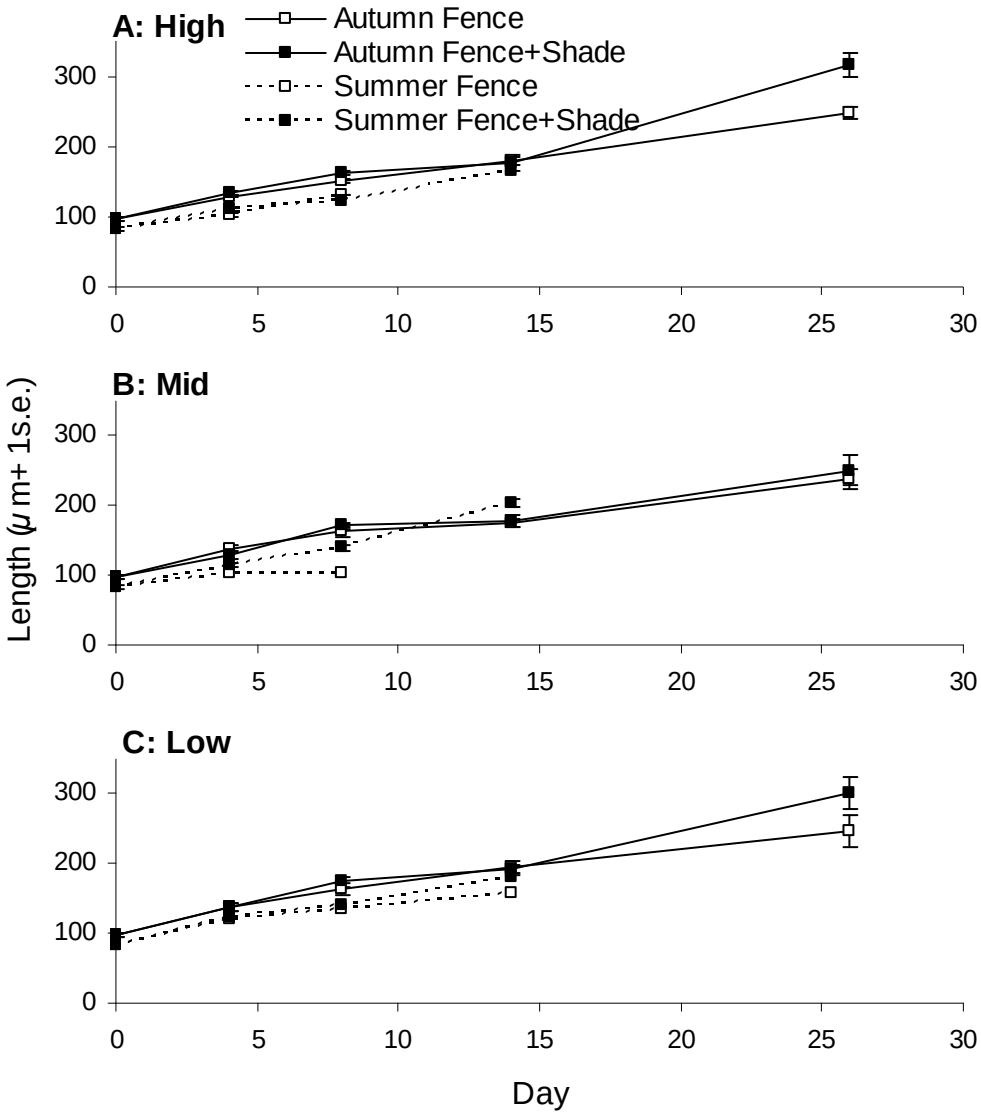


**Figure 4.15** Average lengths of *F. gardneri* germlings transplanted upshore (A: High shore, B: Mid shore, C: Low shore) in Fence and Fence+Shade treatments in summer 2001 (dashed lines) and autumn 2002 (solid lines).

***Fucus gardneri* – Autumn**

In contrast to summer, in autumn there were few significant factors through time. There was similar survival between sites, shore heights and treatments (Fig. 4.16; Table 4.10). Shore height on its own had no significant effect, but there were significant site x shore height interactions on Day 4 and Day 26 which were due to survival at each shore height being different between sites. In general, germlings at Fogarty Creek had better survival than Depoe Bay.

Maximum temperatures were higher at Depoe Bay than at Fogarty Creek, and were 34.5°C and 32.5°C in the high and low shores respectively (c.f. 27°C and 22.5°C at Fogarty Creek high and low shores respectively). The high shores had consistently higher temperatures than the mid and low shores (Fig. 4.6, C,D; Fig. 4.16).

In contrast to the summer experiment, sizes were never significantly different between shore heights. Treatment effects were significant on Day 8 ($F_{1,28}$=4.518 $p$<0.05) and Day 26 ($F_{1,26}$=8.899 $p$<0.01), with longer germlings in the shaded treatments (Fig. 4.15).

There were significant differences in survival of fenced treatments between seasons at Day 14 ($F_{2,30}$=48.73114 $p$<0.05). Survival was much better across all shore heights during autumn than in summer (Tukey HSD high autumn vs. high summer $p$<0.001; mid autumn vs. mid summer $p$<0.01; low autumn vs. low summer $p$<0.01). It is difficult to compare sizes between seasons due to the lack of surviving summer germlings. By Day 14, growth was not significantly different between seasons in low shore fenced treatments.

**Table 4.10** ANOVA results of *F. gardneri* survival across sites, shore heights, grazing and heat stress/desiccation treatments in autumn 2002. Sites were treated as random. Cochran's tests were non-significant for all days except Day 26. Day 26 data were square-root transformed to stabilize variances. * $P$<0.05, ** $P$<0.01, *** $P$<0.001.

| | | Day 1 | | Day 4 | | Day 8 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 0.2 | 0 | 328.5 | 0.066 | 35.6 | 0.065 |
| Shore Height (SH) | 2 | 13.0 | 0 | 4592.3 | 0.435 | 737.3 | 1.792 |
| Treatment (TMT) | 4 | 251.4 | 2 | 1364.2 | 1.655 | 122.3 | 0.539 |
| Site*SH | 2 | 584.7 | 1 | **5280.9** | **11.272**** | 411.3 | 4.378 |
| Site*TMT | 4 | 138.4 | 0 | 206.1 | 0.440 | 226.9 | 2.418 |
| SH*TMT | 8 | 284.7 | 0 | 225.1 | 0.480 | 131.1 | 1.400 |
| Site*SH*TMT | 8 | 603.0 | 2 | 468.5 | 1.003 | 93.6 | 0.275 |
| Error | 60 | 325.4 | | 467.2 | | 340.5 | |

| | | Day 14 | | Day 26 | |
|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* |
| Site | 1 | 1816.92 | 3.19 | 26.67 | 1.40 |
| Shore Height (SH) | 2 | 404.14 | 1.11 | 29.71 | 0.79 |
| Treatment (TMT) | 4 | 152.52 | 0.46 | 8.17 | 1.81 |
| Site*SH | 2 | 364.07 | 2.82 | **37.78** | **20.10***** |
| Site*TMT | 4 | 334.25 | 2.59 | 4.51 | 1.20 |
| SH*TMT | 8 | 227.20 | 1.76 | 4.88 | 0.65 |
| Site*SH*TMT | 8 | 128.97 | 0.96 | 7.51 | 0.74 |
| Error | 60 | 133.68 | | 73.19 | |

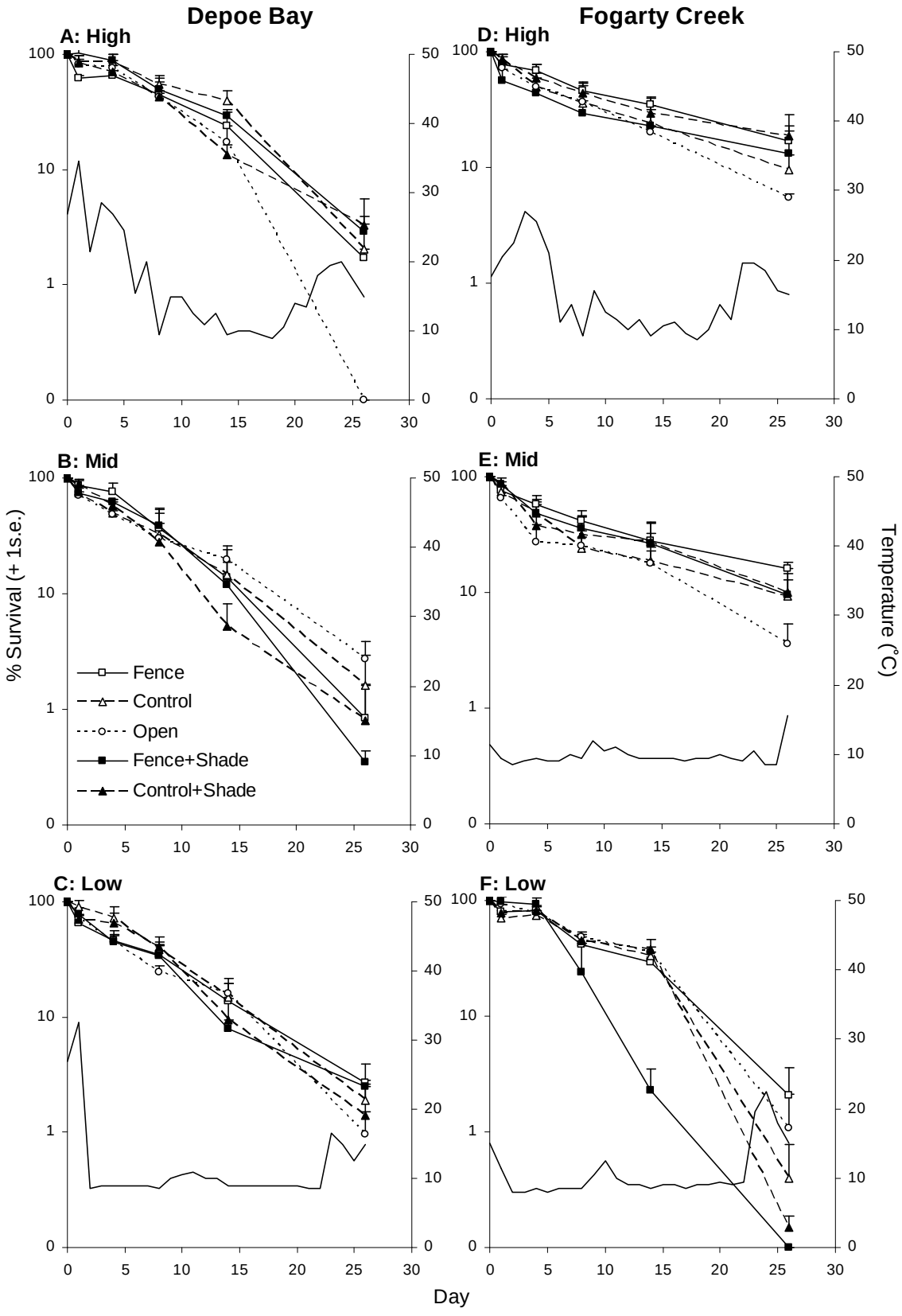


**Figure 4.16** Autumn 2002, Oregon. Percent survival of *F. gardneri* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at Depoe Bay (A-C) and Fogarty Creek (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis. Temperature data logger was lost from Depoe Bay mid shore.

***Pelvetiopsis limitata* – Spring**

There were significant site x shore height x treatment interaction effects on the survival of *P. limitata* on all monitoring days (Fig. 4.17; Table 4.11). Shade enhanced survival in the high shore at both sites and at the mid shore at Fogarty Creek, but had no effect on the low shore germlings and had a detrimental effect on the mid shore germlings at Depoe Bay. Although % survival was relatively low by Day 14 (average 14% survival), germlings survived at both sites in all treatments and at all shore heights, with the exception of the open treatments on the high shore at Fogarty Creek.

Maximum temperatures were consistently high across shore heights and sites for the duration of the experiment, with maxima of 38.5°C, 36.5°C and 34°C in the high, mid and low shores respectively (Fig. 4.6, E,F; Fig. 4.17). Maximum temperatures were rarely below 20°C.

Sizes were significantly different between shore heights on Day 8 ($F_{2,27}$=3.591, $p$<0.05) and Day 14 ($F_{2,28}$=6.297, $p$<0.01) (Fig. 4.18). The largest germlings were on the high shore and smallest germlings were on the low shore. There was a significant shore height x treatment interaction effect on Day 8 ($F_{2,27}$=10.535, $p$<0.001) because shade enhanced growth in the high and mid shores, but had a negative or no effect on the low shore (Fig. 4.15, C).

**Table 4.11** ANOVA results of *P. limitata* survival across sites, shore heights, grazing and heat stress/desiccation treatments in spring 2002. Sites were treated as random. Cochran's tests were significant for Day 1, and non-significant for all other days. Day 1 data were arcsine-transformed to stabilize variances. * $P$<0.05, ** $P$<0.01, *** $P$<0.001.

| | | Day 1 | | Day 4 | | Day 8 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 0.062 | 0.219 | 4403.5 | 3.090 | 3204.95 | 7.922 |
| Shore Height (SH) | 2 | 0.481 | 2.311 | 216.8 | 0.116 | 130.60 | 0.210 |
| Treatment (TMT) | 4 | 0.282 | 0.564 | 496.7 | 1.268 | 712.26 | 1.803 |
| Site*SH | 2 | 0.208 | 0.494 | 1872.8 | 2.231 | 622.85 | 1.016 |
| Site*TMT | 4 | 0.499 | 1.185 | 391.8 | 0.467 | 395.03 | 0.644 |
| SH*TMT | 8 | 0.179 | 0.424 | 515.3 | 0.613 | 422.63 | 0.688 |
| Site*SH*TMT | 8 | **0.421** | **4.232*** ** | **840.0** | **2.486*** | **614.00** | **5.241*** ** |
| Error | 60 | 0.100 | | 337.9 | | 117.15 | |

| | | Day 14 | |
|---|---|---|---|
| Factor | df | MS | *F* |
| Site | 1 | 1014.68 | 2.344 |
| Shore Height (SH) | 2 | 136.37 | 0.353 |
| Treatment (TMT) | 4 | 960.74 | 3.883 |
| Site*SH | 2 | 386.86 | 1.928 |
| Site*TMT | 4 | 247.45 | 1.232 |
| SH*TMT | 8 | 165.44 | 0.823 |
| Site*SH*TMT | 8 | **201.36** | **2.205*** |
| Error | 60 | 91.32 | |

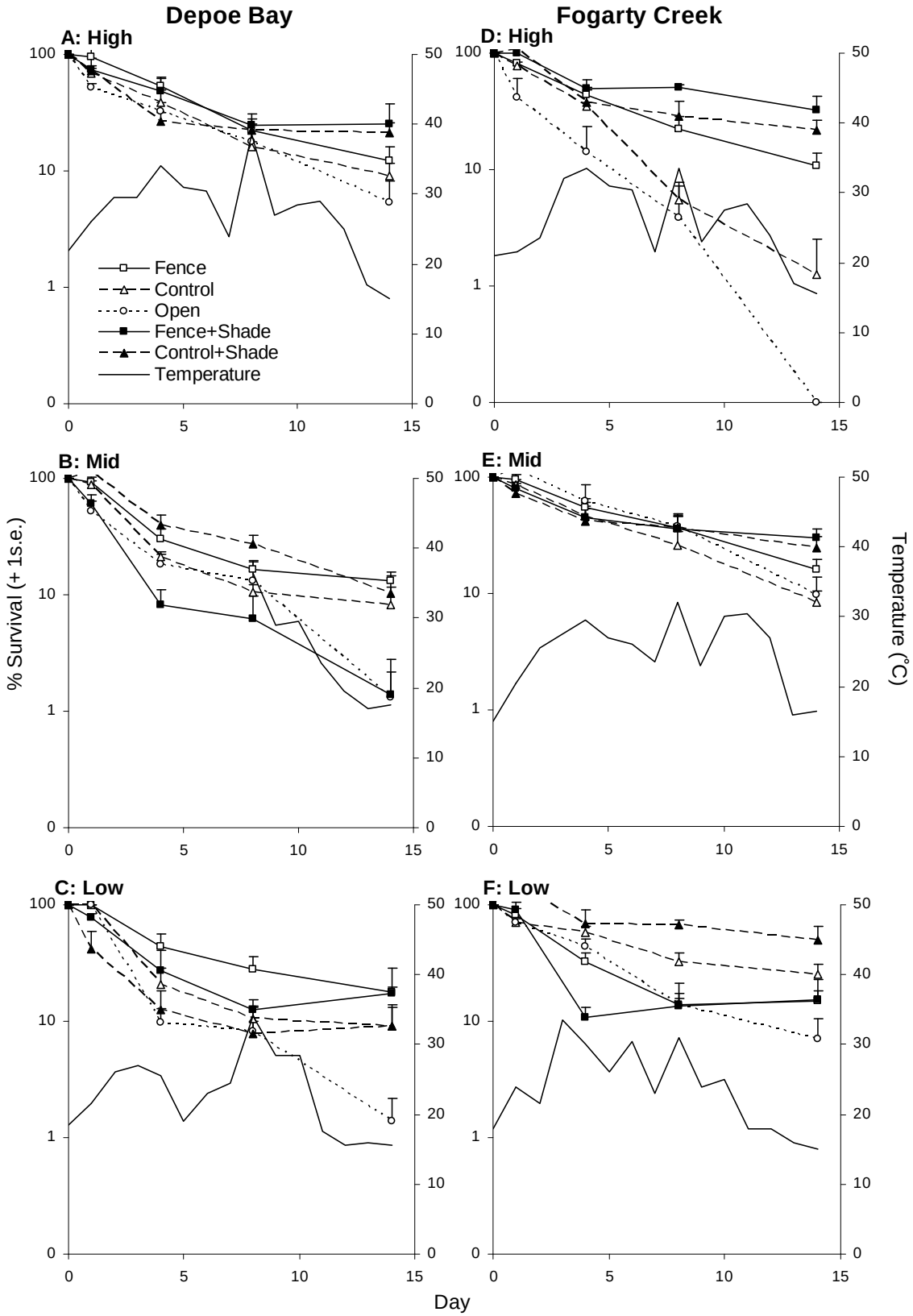


**Figure 4.17** Spring 2002, Oregon. Percent survival of *P. limitata* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at Depoe Bay (A-C) and Fogarty Creek (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis.

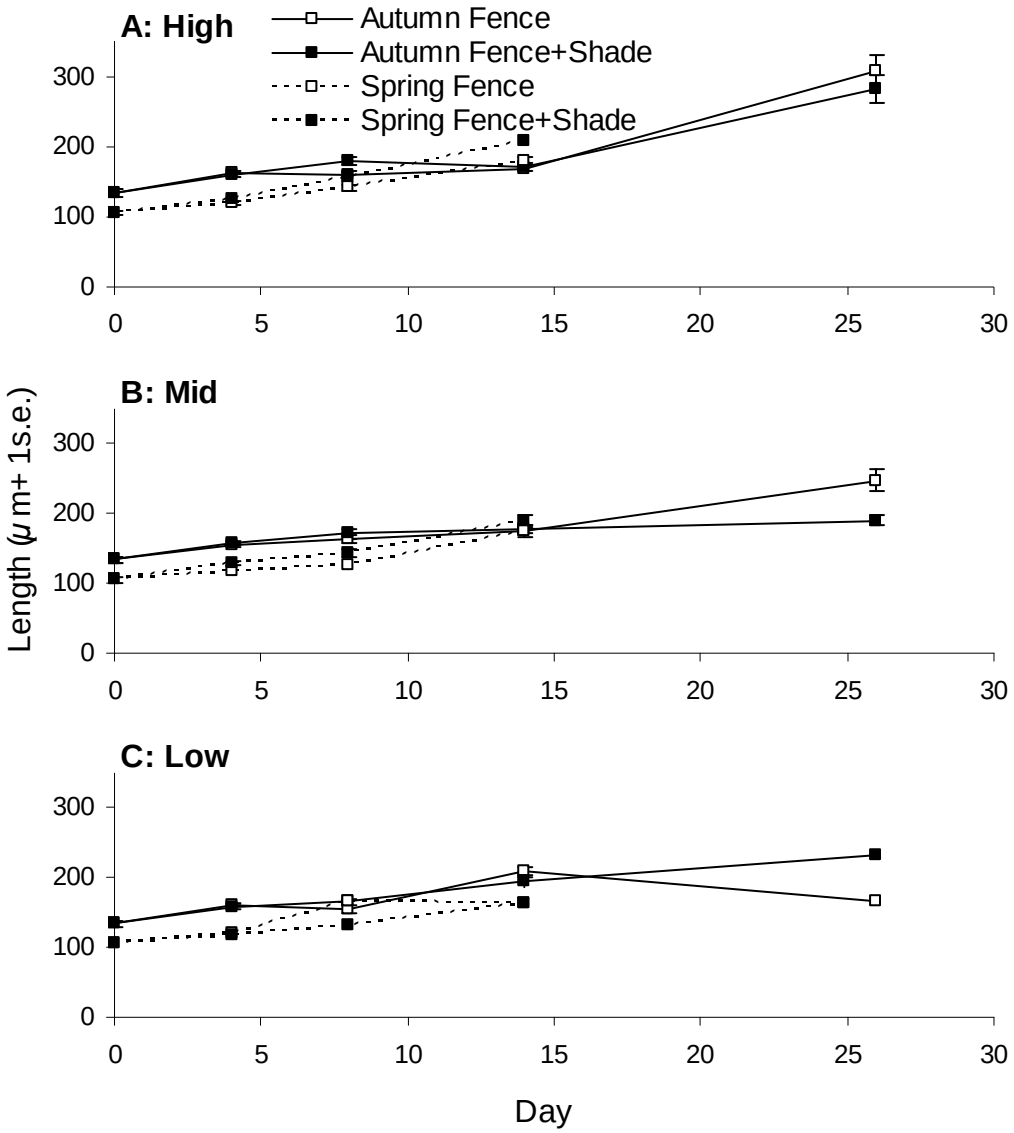


**Figure 4.18** Average lengths of *P. limitata* germlings transplanted upshore (A: High shore, B: Mid shore, C: Low shore) in Fence and Fence+Shade treatments in spring 2002 (dashed lines) and autumn 2002 (solid lines).

***Pelvetiopsis limitata* – Autumn**

In autumn, there were significant interaction effects on all monitoring days after Day 1, but significant treatment effects only on Day 4 (Table 4.12). High shore germlings had better survival than mid and low shore germlings (Fig. 4.19). By Day 26, only germlings in the high shore at Depoe Bay, and in the high and mid shore at Fogarty Creek survived.

Maximum temperatures were higher at Depoe Bay than at Fogarty Creek (34.5°C and 32.5°C in the high and low shores respectively at Depoe Bay compared with 27°C and 22.5°C at Fogarty Creek high and low shores respectively). The high shores had consistently higher temperatures than the mid and low shores (Fig. 4.6, C, D; Fig. 4.19). Temperatures were considerably lower than during the spring experiment.

Sizes were significantly different between shore heights on Day 14 in autumn ($F_{2,26}$=8.419, $p$<0.01). In contrast to the spring experiment, largest germlings were in the low shore, and smallest were in the high shore (Fig. 4.18). Shade had no significant effect. On Day 26, using data from only the high and mid shores (only 2 plants remained in the low shore), the effect of shore height was again significant ($F_{1,8}$=7.2528, $p$<0.05), with mid shore fence+shade germlings significantly smaller than the rest (Tukey HSD $p$<0.05).

There were no significant differences in survival of fenced treatments between seasons at Day 14. Growth was not significantly different between seasons, but there was a significant season x shore height interaction ($F_{2,28}$=6.3779, $p$<0.01) because growth was variable between shore heights during each experiment.

The *P. limitata* autumn experiment occurred at the same time as the *F. gardneri* autumn experiment, which allows an excellent species comparison because the germling were exposed to the same conditions. There were significant differences in survival of fenced treatments between species on Day 14 ($F_{2,28}$=13.8658, $p$<0.001). In general, *F. gardneri* had better survival than *P. limitata*, and site, shore height and treatment had less effect.

**Table 4.12** ANOVA results of *P. limitata* survival across sites, shore heights, grazing and heat stress/desiccation treatments in autumn 2002. Sites were treated as random. Cochran's tests were significant on Days 8 and 14. Variances could not be stabilized but square root transformed data gave more conservative p-values. * $P$<0.05, ** $P$<0.01, *** $P$<0.001.

| | | Day 1 | | Day 4 | | Day 8 | |
|---|---|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* | MS | *F* |
| Site | 1 | 264.0 | 0.1861 | 2291.64 | 2.12519 | 36.664 | 1.65467 |
| Shore Height (SH) | 2 | 228.3 | 0.2135 | 1153.18 | 1.12048 | 32.289 | 1.41561 |
| Treatment (TMT) | 4 | 289.8 | 0.5043 | **853.41** | **7.84915*** | 8.847 | 6.14848 |
| Site*SH | 2 | 1069.3 | 4.7417 | **1029.18** | **17.27232**** | **22.810** | **10.90602**** |
| Site*TMT | 4 | 574.6 | 2.5481 | 108.73 | 1.82470 | 1.439 | 0.68773 |
| SH*TMT | 8 | 422.1 | 1.8719 | **256.55** | **4.30548*** | 3.382 | 1.61609 |
| Site*SH*TMT | 8 | 225.5 | 0.6151 | 59.59 | 0.28508 | 2.093 | 1.14942 |
| Error | 60 | 366.7 | | 209.01 | | 1.821 | |

| | | Day 14 | | Day 26 | |
|---|---|---|---|---|---|
| Factor | df | MS | *F* | MS | *F* |
| Site | 1 | 0.7366 | 0.0509 | 93.6897 | 0.909392 |
| Shore Height (SH) | 2 | 16.0572 | 1.2034 | 192.0127 | 1.821109 |
| Treatment (TMT) | 4 | 4.1104 | 1.5454 | 34.8430 | 0.649330 |
| Site*SH | 2 | **13.3429** | **9.2452**** | 105.4372 | 1.891092 |
| Site*TMT | 4 | 2.6597 | 1.8419 | 53.6598 | 0.957522 |
| SH*TMT | 8 | 3.7207 | 2.5652 | 40.2507 | 0.703326 |
| Site*SH*TMT | 8 | 1.4504 | 1.1491 | **57.2291** | **2.757522*** |
| Error | 60 | 1.2622 | | 20.7538 | |

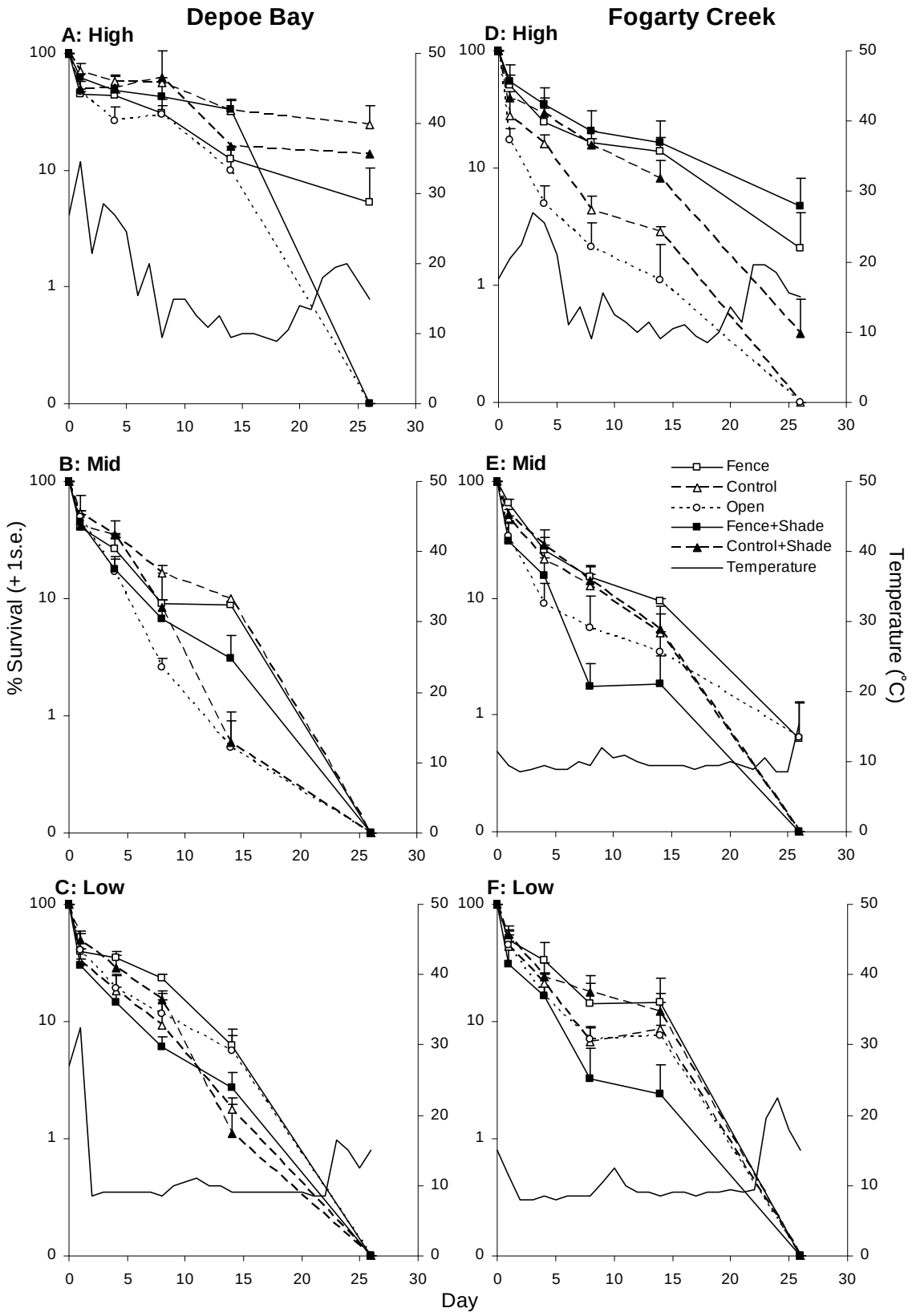


**Figure 4.19** Autumn 2002, Oregon. Percent survival of *P. limitata* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at Depoe Bay (A-C) and Fogarty Creek (D-F). Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis. Temperature data logger was lost from Depoe Bay mid shore.

### 4.3.4 Comparative survival and growth across species

***Major Factors***

A major feature of these experiments was that the survival and growth of New Zealand species were strongly affected by grazing, heat/desiccation stress, shore height and season. Shore height, treatment and interaction terms were often significant. In contrast, factors in the Oregon experiments rarely had significant effects, and in general effects were much weaker. A summary of significant effects at Day 14 shows treatment was always significant in New Zealand experiments, and this was due to strong grazing and/or desiccation effects (Table 4.13). In Oregon, treatment was significant only in the *F. gardneri* summer experiment, where there was an overwhelming effect of shade (Table 4.13, Fig. 4.14).

A summary of effects on survival (Table 4.14) shows all experiments had better survival in cooler seasons. Survival was higher in the low shore in New Zealand due to strong heat/desiccation stress in the high and mid shores. In contrast, survival was generally better in the high shore in Oregon. The exception to this was the *F. gardneri* summer experiment, in which all mid and high shore germlings died unless they were in shaded treatments. Grazing was important in the low shore in New Zealand experiments, but had variable and much weaker effects in Oregon. Growth was faster in the low shore and in warmer seasons in New Zealand, but was not significantly different between seasons or shore height in Oregon.

**Table 4.13** Significant ANOVA results at Day 14 for each species. **P*<0.05, ***P*<0.01, ***P*<0.01.

| | New Zealand | | | | Oregon | | | |
|---|---|---|---|---|---|---|---|---|
| | *H. banksii* | | *D. antarctica* | | *F. gardneri* | | *P. limitata* | |
| | Autumn | Summer | Winter | Spring | Autumn | Summer | Autumn | Spring |
| Site | | | | | | | | |
| Shore Height | | * | | | | | | |
| Treatment | * | ** | * | ** | | ** | | |
| Site*SH | * | *** | * | | | | ** | |
| Site*TMT | | | | | | | | |
| SH*TMT | * | *** | | | | | | |
| Site*SH*TMT | | | | | | | | * |

**Table 4.14** Summary of factors affecting survival of New Zealand and Oregon species. ↑ = increased survival, ↓ = decreased survival. Bold text indicates strong effects.

| | New Zealand | | Oregon | |
|---|---|---|---|---|
| | *H. banksii* | *D. antarctica* | *F. gardneri* | *P. limitata* |
| Season | ↑ **cooler** | ↑ **cooler** | ↑ **cooler** | ↑ cooler |
| Shore Height | ↑ **Low** | ↑ **Low** | Summer ↑ Low<br>Autumn ↑ High | ↑ High |
| Heat/Desiccation Stress | ↓**High, Mid** | ↓**High, Mid** | ↓ **High, Mid in Summer** | ↑ High |
| Grazing | ↓ **Low** | ↓ **Low** | ↓ High, Low in Summer<br>↓ Mid in Autumn | ↓ High, Mid in spring<br>↓ Low in Autumn |

***Heat/Desiccation Stress***

A percent shade effect was calculated by subtracting the average fence survival from the average fence + shade survival for each monitoring day (Fig. 4.20). Generally, the provision of shade enhanced survival in the high shore. The effect was particularly strong in the *F. gardneri* summer (Fig. 4.20, E) and *D. antarctica* experiments (Fig. 4.20, C, D). Mid shore survival was enhanced with shade in warmer conditions, but shade often had neutral or negative effects in cooler conditions. The effect of shade in the low shore was also often negative. These negative effects were consistent in the mid and low shore *P. limitata* experiments (Fig. 4.20).

After 2 weeks, survival in fenced treatments was better downshore for New Zealand species, but the effect of shore height was not significant for Oregon species (Fig. 4.21, A). Survival of low shore germlings was not significantly different between species. After 1 month, *H. banksii* germlings had higher survival than other species in the mid and low shores in autumn and in the low shore in summer (Fig. 4.21, B). However, *H. banksii* had 0% survival in the high shore, regardless of season or treatment. Interestingly, the low shore species *D. antarctica* had germling survival in the high shore, and shade enhanced survival (Fig 4.21; Fig. 4.22). Oregon species also had relatively good survival in the high shore. The only experiments that were monitored after approximately 2 months were *H. banksii* autumn and *D. antarctica* winter and spring experiments. After 2 months, *H. banksii* had best survival (Fig. 4.21, C; Fig. 4.22, C). Survival of *D. antarctica* germlings was enhanced by shade, and shaded treatments in the high shore in winter had highest survival.

Although percent survival for some species was low after 2 weeks, when converted to actual numbers per $cm^2$, survival ranged from approximately 1-2 germlings per $cm^2$ (for *P. limitata*) to 745 germlings per $cm^2$ (for *D. antarctica* winter low shore fenced treatments) (Fig. 4.23). Species that had the highest initial settling densities also had the highest number surviving after 2 weeks.

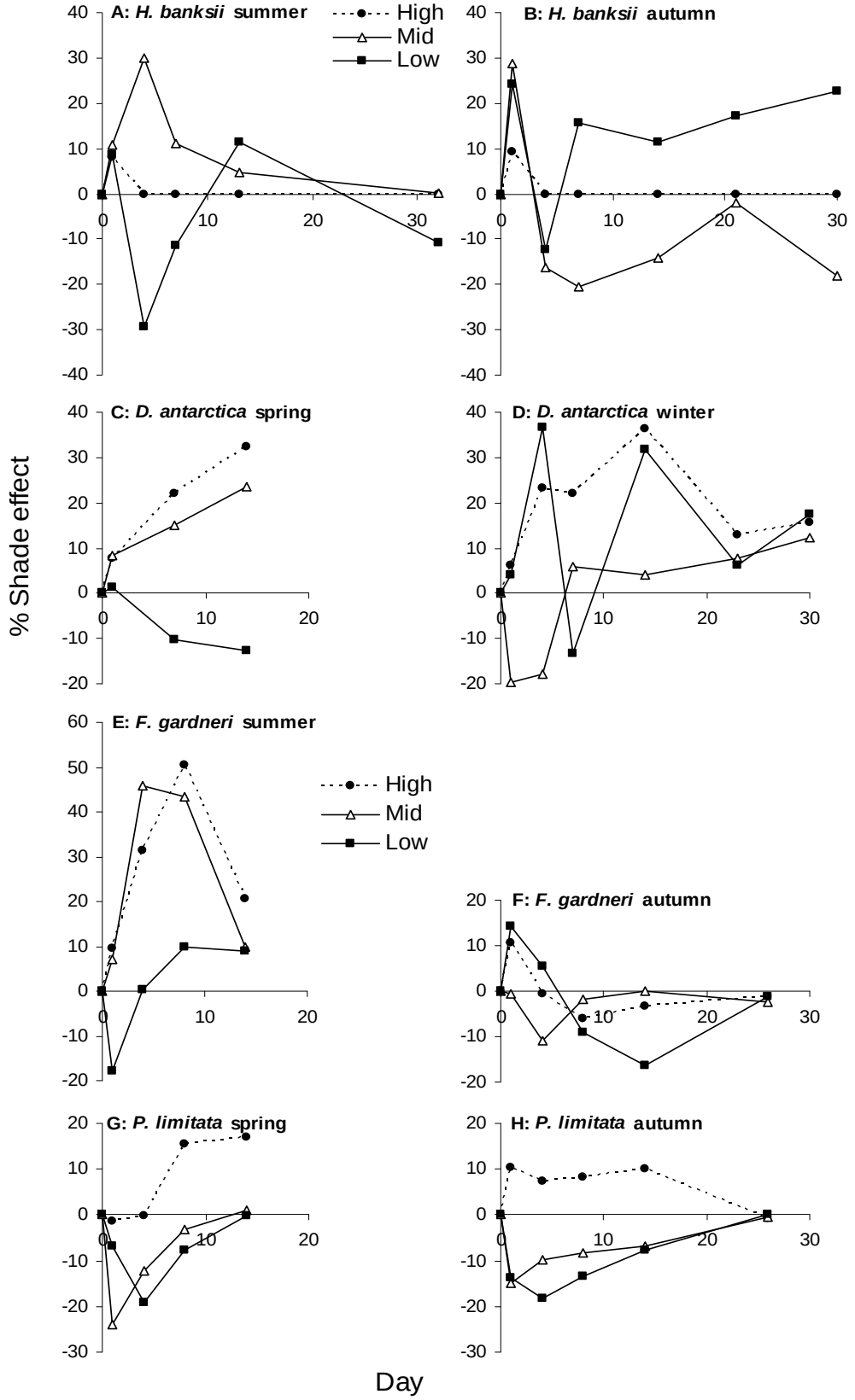


**Figure 4.20** Percent shade effect on survival across shore heights through time in the A, B: *H. banksii* summer and autumn, C, D: *D. antarctica* spring and winter, E, F: *F. gardneri* summer and autumn, and G, H: *P. limitata* spring and autumn experiments. Calculated by subtracting the percent survival in the fence treatments from the fence + shade treatments.

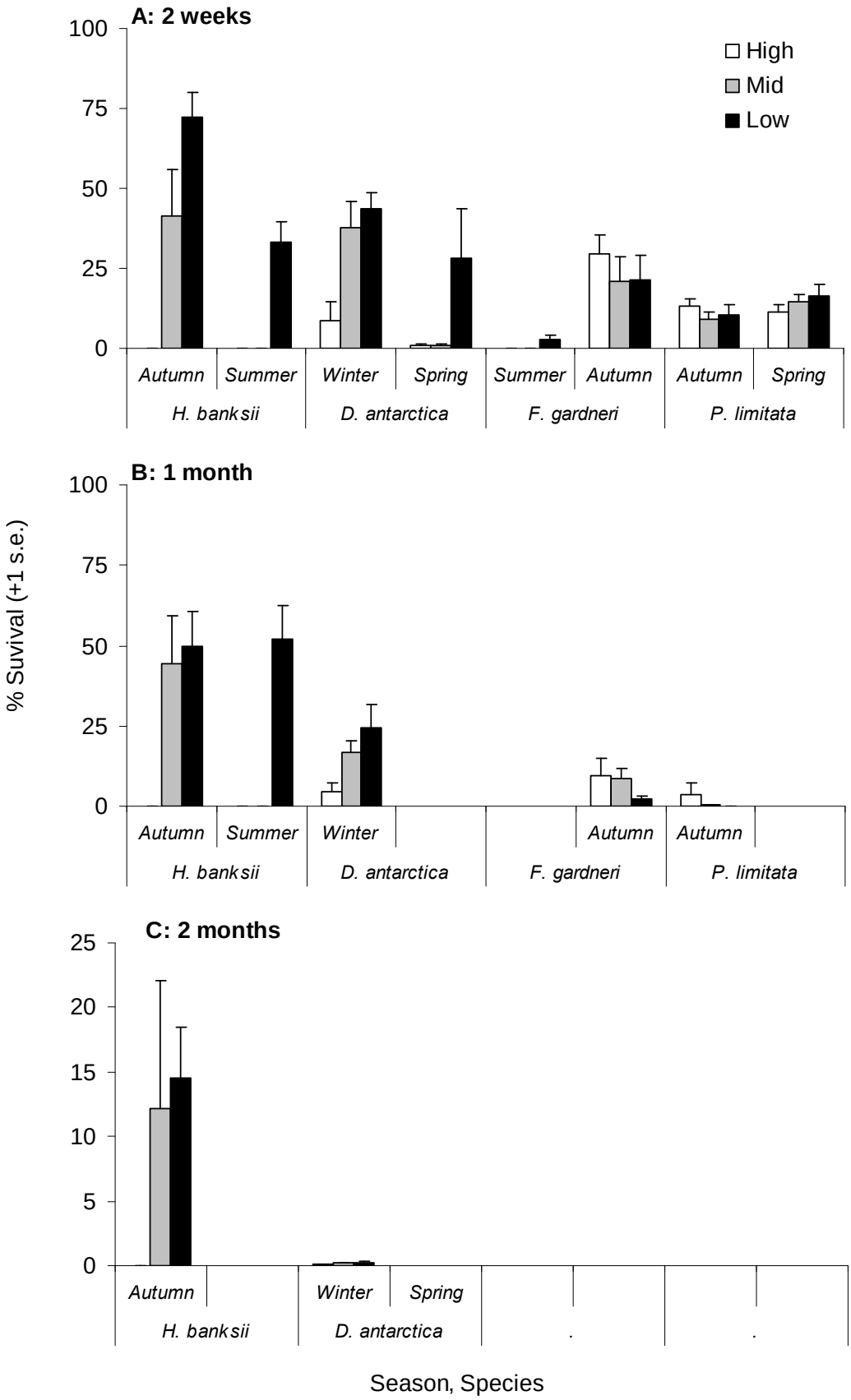


**Figure 4.21** Comparative survival of *H. banksii, D. antarctica, F. gardneri* and *P. limitata* in fence treatments in the high, mid and low shore after approximately A: 2 weeks, B: 1 month, and C: 2 months.

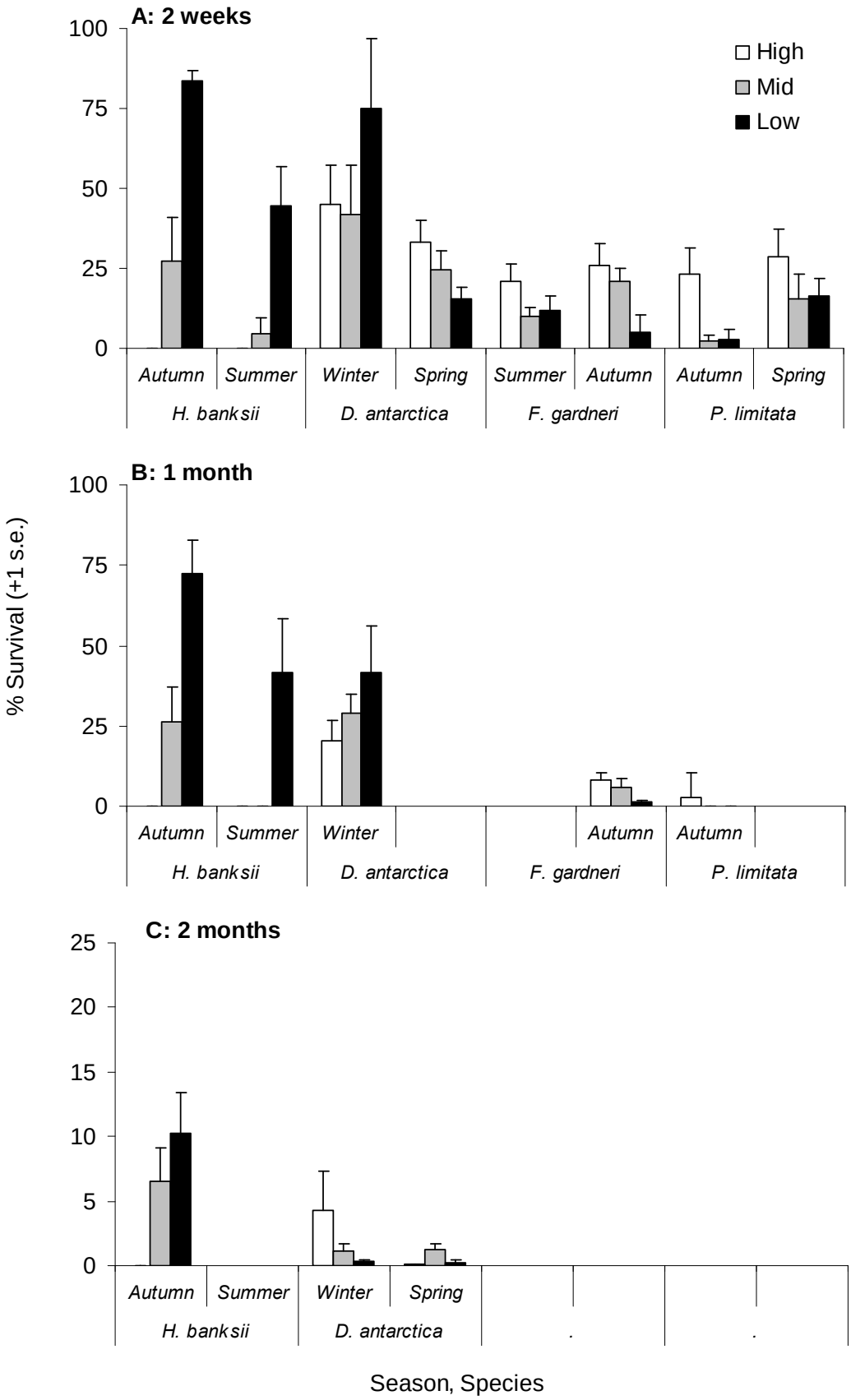


**Figure 4.22** Comparative survival of *H. banksii, D. antarctica, F. gardneri and P. limitata* in fence + shade treatments in high, mid and low shore heights after approximately A: 2 weeks, B: 1 month, and C: 2 months.

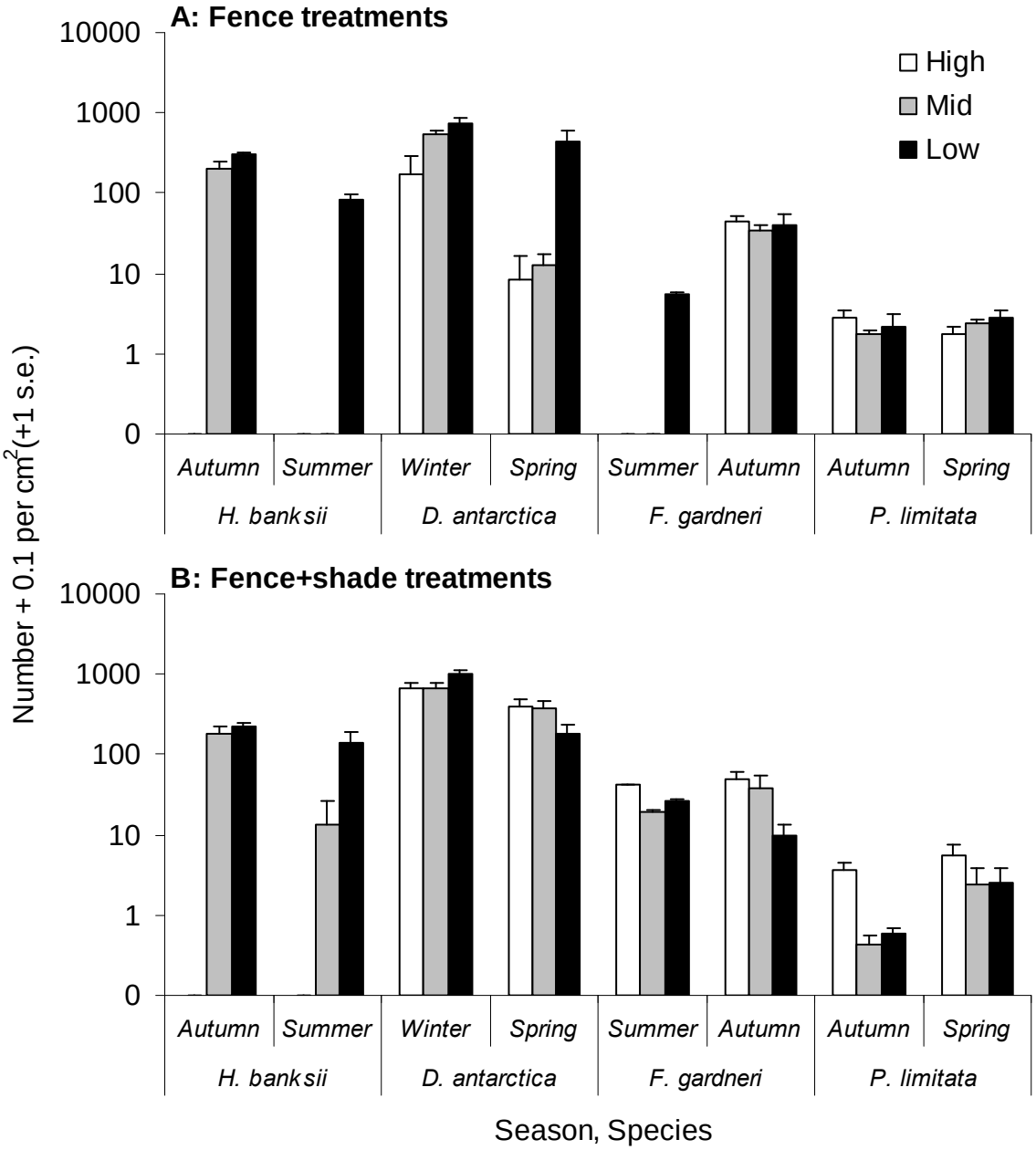


**Figure 4.23** Comparative numbers of germlings (+0.1) per $cm^2$ of *H. banksii, D. antarctica, F. gardneri and P. limitata* in high, mid and low shore heights after 2 weeks in A: Fence treatments, and B: Fence+shade treatments.

***Grazing effects***

The effects of grazers were evident on most open and fence control treatments, with distinct grazer trails where grazers had removed germlings and any sediment and ephemeral algal growth (Fig. 4.24). However, effects were highly variable between species, season and through time (Fig. 4.25). In general, in New Zealand, grazing was most intense on the low shore (Fig. 4.25, A-D). This was particularly strong in the *H. banksii* experiments, with at least 40% of a grazing effect after one month (Fig. 4.25, A, B). In autumn, the mid shore also showed a positive grazing effect. Negative grazing effects in the early monitor days in the

high and mid shores in the summer experiment, and the high shore in the autumn experiment were due to higher survival in fence controls than fence treatments.

In Oregon, slight grazing effects were evident on *F. gardneri* in summer in the first week (Fig. 4.25, E). In spring there were positive grazing effects on *P. limitata* in the high and mid shores, but negligible or no effects in the low shore (Fig. 4.25,G). In autumn, there were positive grazing effects on mid shore *F. gardneri*, and low shore *P. limitata* germlings, but low or slightly negative grazing effects in other shore heights (Fig. 4.25, F, H).

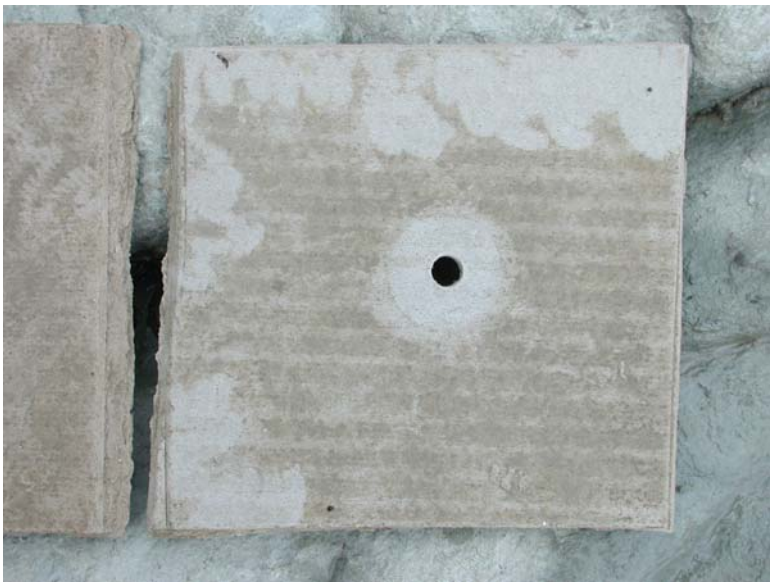

**Figure 4.24** An open treatment from the *H. banksii* summer experiment showing grazing trails on the top and left edge of the plate.

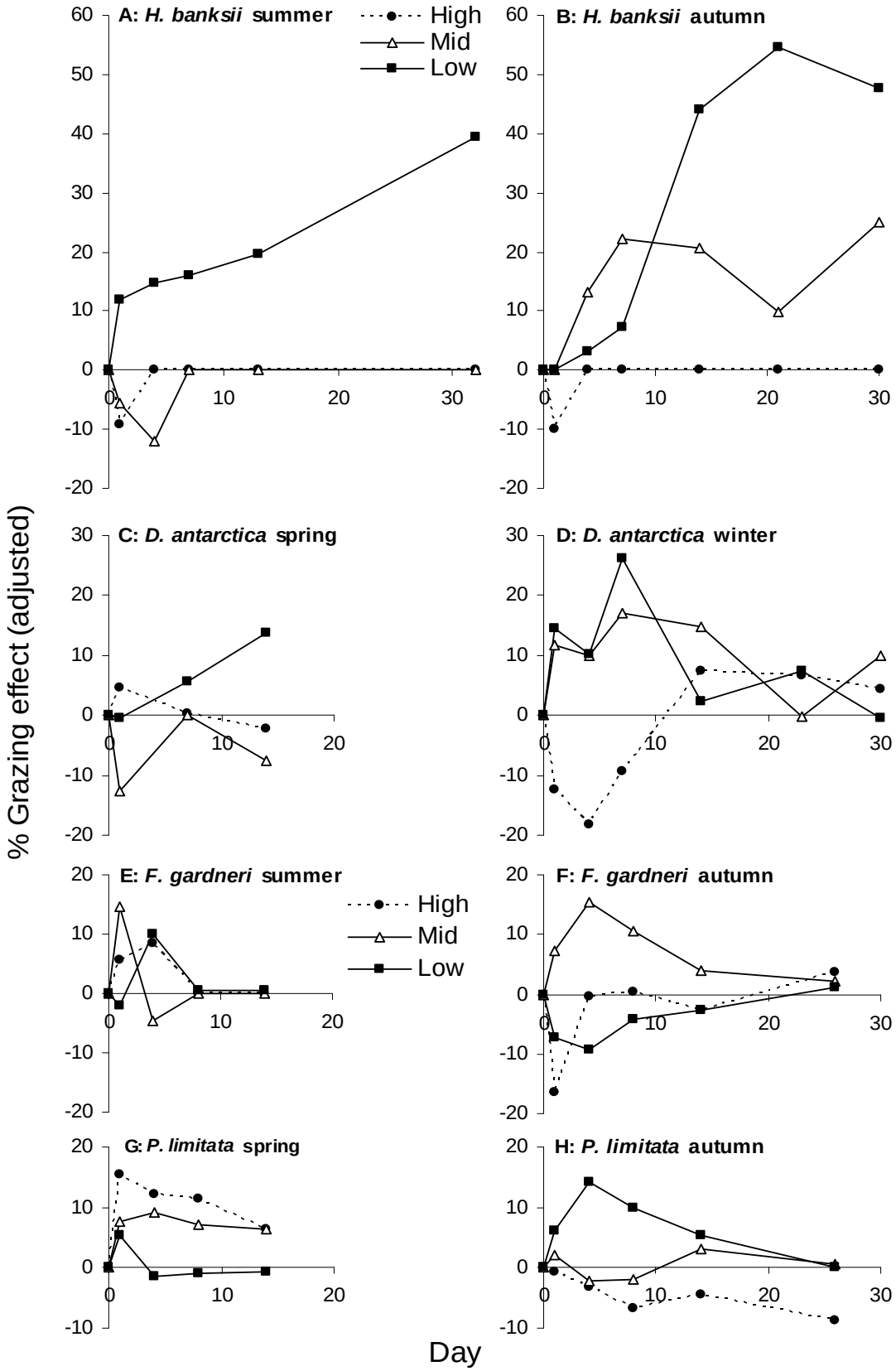


**Figure 4.25** Percent grazing effect (adjusted for fence effect) across shore heights through time in the A, B: *H. banksii* summer and autumn, C, D: *D. antarctica* spring and winter, E, F: *F. gardneri* summer and autumn, and G, H: *P. limitata* spring and autumn experiments. Calculated by subtracting the percent mortality in the fence treatments from the open treatments, and adjusting for the 'fence effect' by subtracting the difference between the mortality on open plates and fence control plates.

***Growth***

Growth was not significantly different between species for low shore fenced treatments on Day 14. In general, growth was faster on the low shore (Fig. 4.26, A), but an exception was *P. limitata* germlings in spring, which grew faster in the high shore. Spring low shore *D. antarctica* germlings attained the greatest lengths.

After 1 month, low shore *H. banksii* summer germlings had grown 4x more than autumn germlings, and more than *D. antarctica* winter and Oregon autumn germlings (Fig. 4.26, B). *P. limitata* germlings grew poorly in the low shore, and only 2 plants remained. After 2 months, *H. banksii* autumn germlings had grown less than 200µm, and low shore *D. antarctica* germlings had grown approximately 5x this (Fig. 4.26, C).

Growth under shade was enhanced in the high shore, and had positive or no effects on the mid and low shore (*c.f.* Fig. 4.26; Fig. 4.27). For example, *D. antarctica* grew better when shaded, indicating heat and desiccation stress affected growth. However, there was little difference in *H. banksii* germling growth.

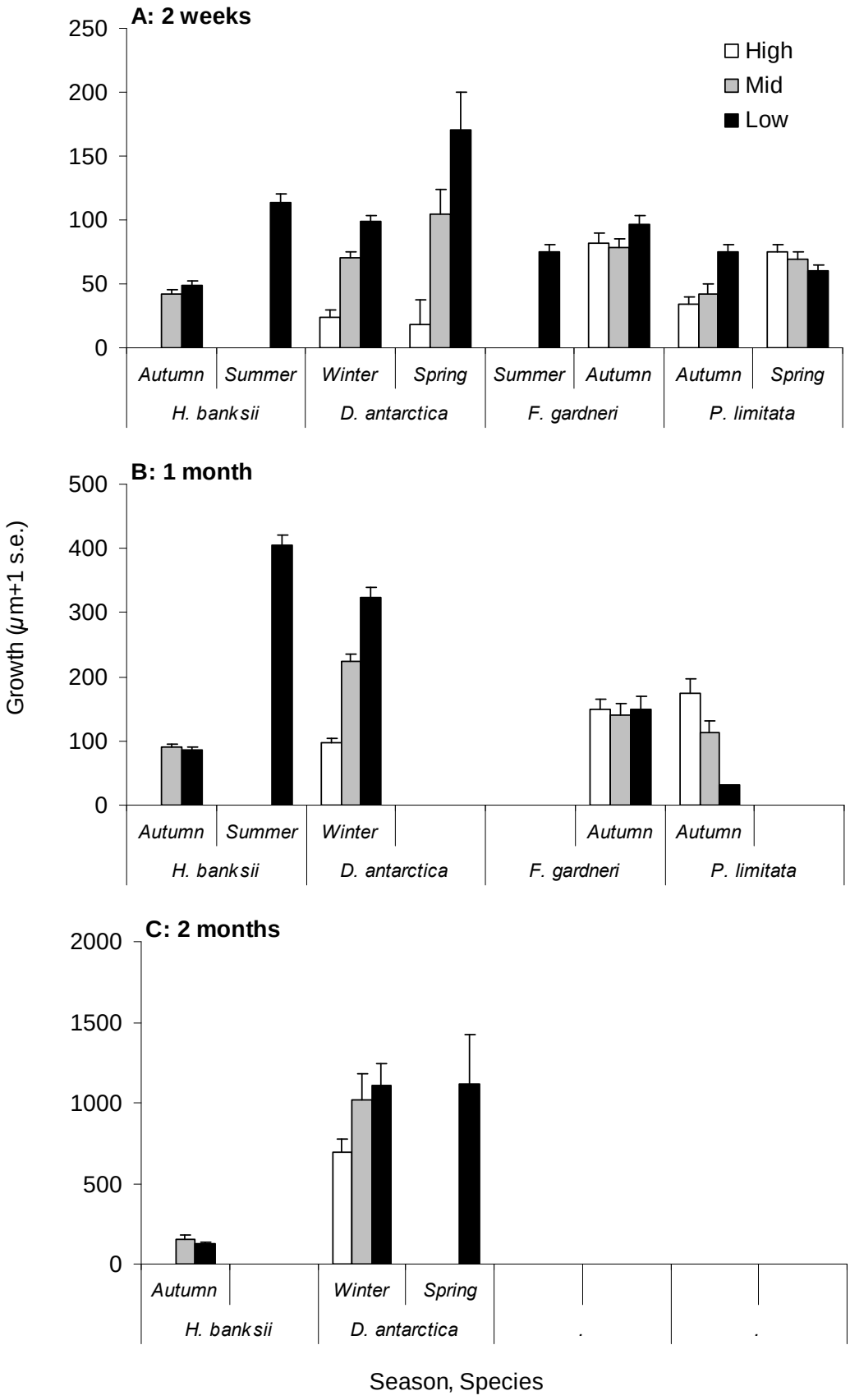


**Figure 4.26** Comparative growth of *H. banksii, D. antarctica, F. gardneri* and *P. limitata* in fence treatments in high, mid and low shore heights after approximately A: 2 weeks, B: 1 month, and C: 2 months.

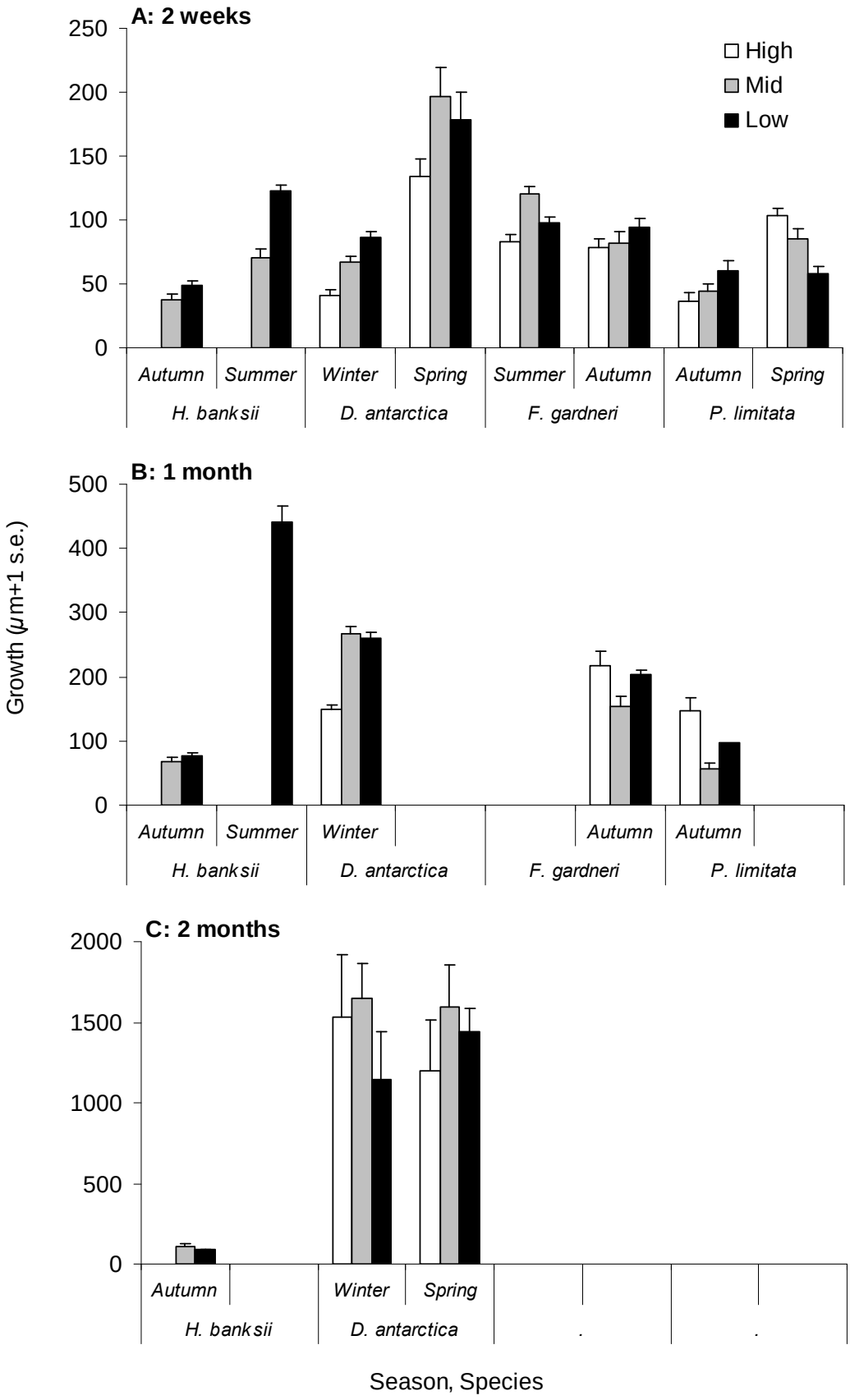


**Figure 4.27** Comparative growth of *H. banksii, D. antarctica, F. gardneri* and *P. limitata* in fence + shade treatments in high, mid and low shore heights after approximately A: 2 weeks, B: 1 month, and C: 2 months.

### 4.3.5 Sediment and ephemeral algae

Sediment was evident only in *H. banksii* experiments. Percent cover and depth of sediment on plates in the low shore at approximately 1 month are shown in Fig. 4.28. Fenced treatments had more sediment than fence controls or open plates (Fig. 4.28; Fig. 4.29).

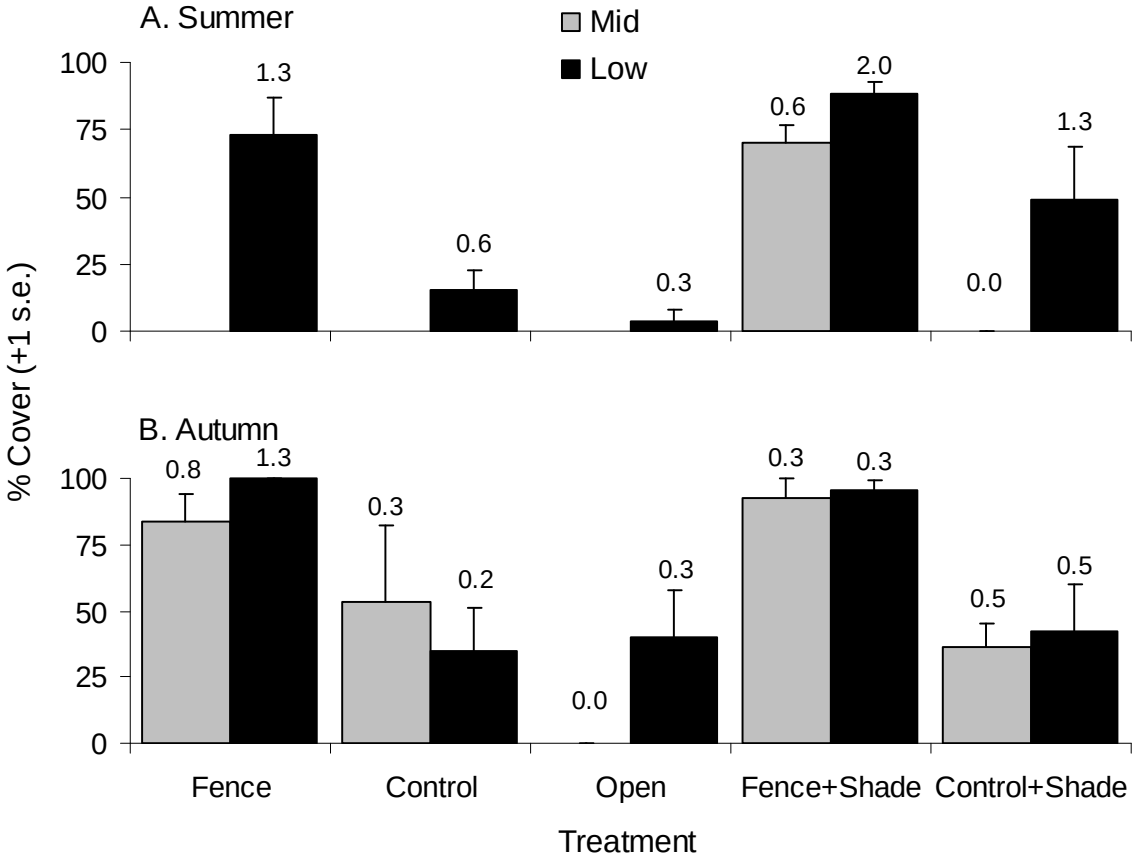


**Figure 4.28** *H. banksii* experiments: average percent cover of sediment on plates in the mid and low shores in A: summer (Day 32), and B: autumn (Day 30), sites combined. In summer, no high shore plates or mid shore plates without shade remained due to death of all germlings. Data labels are average depths of sediment (in mm).

**Figure 4.29** From left to right: fence + shade, fence control + shade, fence, fence control and open treatments from the *H. banksii* summer experiment showing high sediment cover on fenced treatments and little or no sediment on plates that were exposed to grazing.

Ephemeral algal growth was evident by Day 14 in all experiments except during *H. banksii* and *F. gardneri* summer experiments. This growth consisted of unidentified filamentous brown and green algae and diatoms. Algal growth was more dense in fence + shade treatments, and had highest percent covers in mid and low shores (Fig. 4.30). Experiments in cooler months did not necessarily have more filamentous algal growth. For example, the *D. antarctica* winter experiment had filamentous algal growth only in the low shore (Fig. 4.30 B), but experiments in other seasons had filamentous algal growth in the mid and occasionally the high shores (Fig. 4.30 A, C, D, E). In general, algal growth in fenced treatments was thicker and had higher percent cover than on plates that were open to grazing (Fig. 4.30, Fig. 4.31)

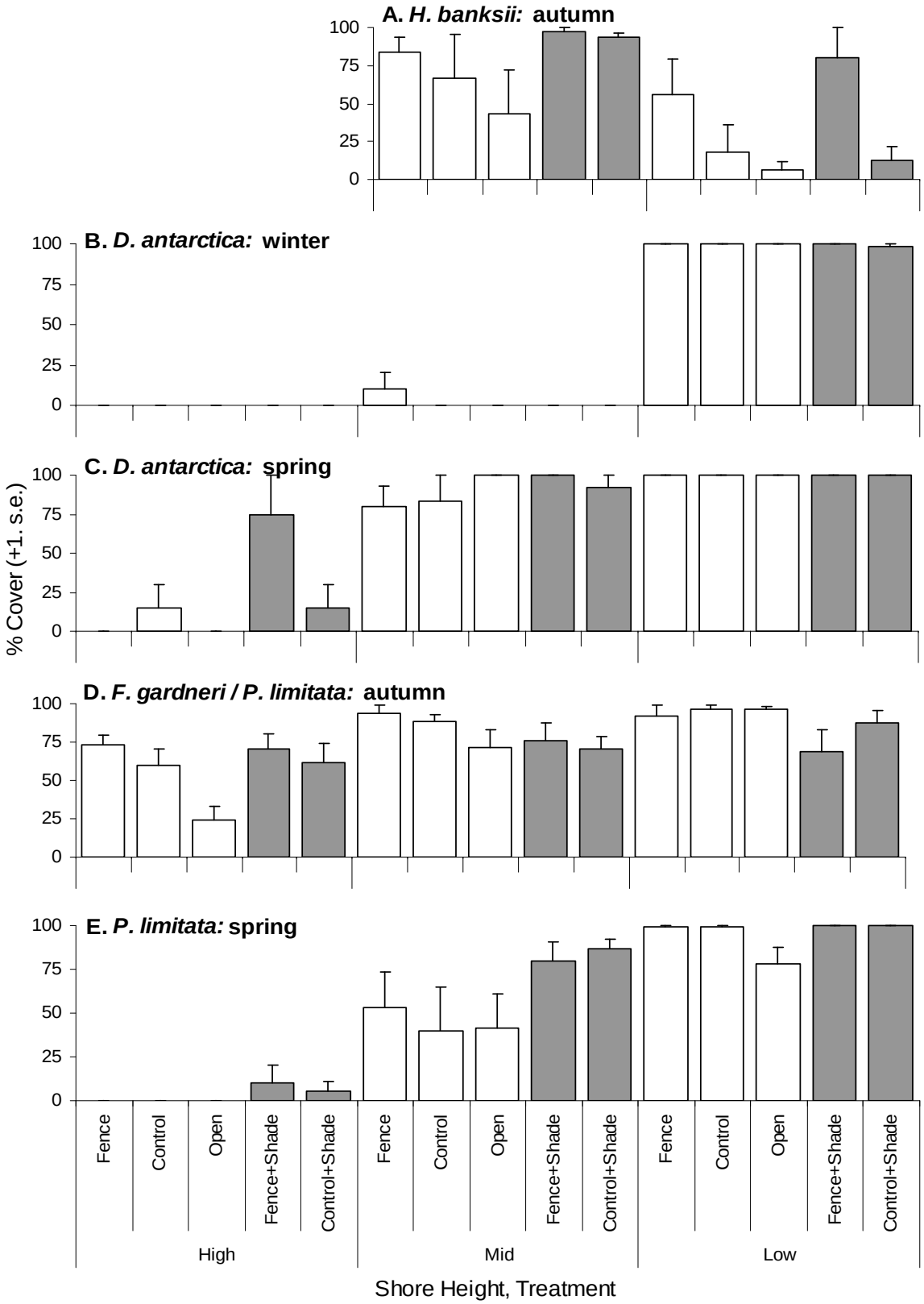


**Figure 4.30.** Percent cover of filamentous brown and green algae and diatoms on plates in each treatment across shore heights at Day 14. No high shore plates were left on the shore in the *H. banksii* autumn experiment due to mortality of all germlings. Shaded bars are shaded treatments. The summer *H. banksii* and *F. gardneri* experiments had no filamentous algal growth after 14 days.

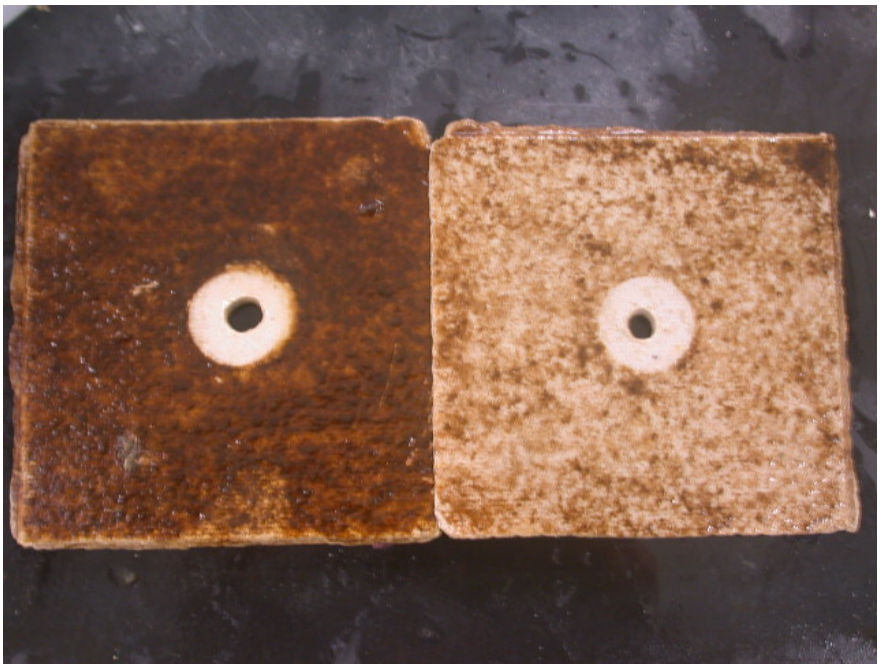

**Figure 4.31** Plates from the *H. banksii* autumn experiment showing dense filamentous brown algal growth on the fenced treatment (left), and sparse growth on the open treatment (right) which had been grazed. The bare circles in the middle of the plates are the areas covered by the washers.

## 4.4 Discussion

### *Overall effects*

The experiments in this chapter tested the relative effects of grazing and heat/desiccation stress on survival and growth of fucoid germlings at different shore heights. High germling mortality was consistent across species, but the rate of mortality depended on conditions and species involved. For example, germlings under stressful conditions (e.g. positioned in the high shore, or experiencing high temperatures) often had 100% mortality in only a few days. This was exemplified by *H. banksii*, which had 100% mortality in high shore treatments after only 4 days. Other shore heights and experiments had slower mortality rates, but often only a fraction of those initially settled remained after 2 weeks. This high mortality during the early life stage is characteristic of fucoid algae. Many physical and biological factors influence survival, but two most commonly cited are heat/desiccation stress and grazing (Santelices 1990, Vadas et al. 1992).

This study found that the relative effects of heat/desiccation stress and grazing were highly variable between species, seasons, sites and shore heights. Despite this temporal and spatial variation, overall differences were evident between hemispheres (Table 4.15). Species in both hemispheres survived better in cooler seasons, but seasonal effects on growth were only significant in New Zealand, where species grew faster in warmer conditions. Shore height had a large effect on New Zealand species, with better survival and growth in the low shore. Shore height had a weak effect on Oregon species, but ultimately low shore germlings had poor survival. New Zealand species had strong effects of grazing in the low shore, and of heat/desiccation in the high and mid shores. Oregon species did not have strong grazing effects, and effects of heat/desiccation stress were generally much weaker.

**Table 4.15** Summary of experimental factors influencing survival and growth of New Zealand and Oregon fucoids. **+/-** strong, +/- weak positive/negative effect on survival or growth; high, mid and low refers to shore height; ND = not determined.

| | New Zealand | | Oregon | |
|---|---|---|---|---|
| Factor | Survival | Growth | Survival | Growth |
| Season | **+ cool** | **+ warm** | +cool | No effect |
| Shore height | **+ low** | **+ low** | + high | + *P. limitata*, high |
| Treatment | | | | |
| Grazing | **- low**<br>**- mid, cool** | ND | +/- variable | ND |
| Heat/desiccation | **- high, mid** | ND | **- *F. gardneri*, high, mid, warm** | ND |

***Heat/Desiccation Stress***

Being exposed on the upper shore was overwhelmingly detrimental to New Zealand species. This effect decreased on the mid shore and was only occasionally important on the low shore. Transplantation upshore not only increased average temperatures, but also increased emersion times at each tidal level, usually by 2 or more hours per tidal level during each low tide period. In all New Zealand experiments, survival and growth was higher in the low shore, and in general survival was enhanced by shade. Intertidal germlings can be highly susceptible to heat and/or desiccation stress (Santelices 1990, Vadas et al. 1992). For instance, studies on *Pelvetia fastigiata* found that germlings experienced sub-lethal and lethal effects, and that microhabitat had an important influence on survival (Brawley & Johnson 1991, Brawley & Johnson 1993, Davison et al. 1993). Photosynthetic rates and embryonic development were impaired after periods of emersion (Davison et al. 1993), and the effect of an adult canopy and a turf habitat also had strong effects. Photosynthetic inhibition and mortality was higher in a turf habitat than in a canopy habitat, and this was related to different intensities of desiccation stress in each microhabitat. It was determined that sub-lethal effects of desiccation can play an important role in recruitment success because they influence competitive interactions or cause germlings to be more susceptible to other sources of mortality (Davison et al. 1993). For New Zealand species, lethal effects of heat/desiccation stress were obvious in high and mid shores. Sublethal stress expressed as slower growth was also observed, and can expose germlings to grazing and competitive interactions for longer periods.

*H. banksii* germlings showed particular susceptibility to heat and desiccation stress, with 100% mortality in the high shore within four days. Even the provision of shade did not enhance survival. Germlings were 'bleached' as reported in other experiments (Brawley & Johnson 1991, Viejo et al. 1999, Dudgeon & Petraitis 2005). Interestingly, compared with *H. banksii*, the low shore species *D. antarctica* had better initial survival in the high shore but was unable to sustain through time. This may have been due to the use of slightly older, and therefore more tolerant, *D. antarctica* germlings at the start of experiments. Germlings can develop tolerances to physical stresses such as UV light, heat and desiccation as they get older (Davison et al. 1993, Henry & Van Alstyne 2004). An experiment at the same sites during summer conditions using 3 week old *H. banksii* germlings had better survival at all shore heights than both 3 and 4 day old *H. banksii* germlings (autumn and summer experiments), and 13 day old *D. antarctica* (spring experiment)(Appendix II). This suggests older germlings are better able to withstand environmental conditions. It also suggests *H. banksii* germlings may be more tolerant of physical stress than *D. antarctica* germlings, because although 1

week older, the *H. banksii* germlings experienced much higher heat/desiccation stress and still had better survival (cf. experimental temperatures Fig. 4.13 and Appendix II).

Shade enhanced survival of high and mid shore *D. antarctica*, indicating that with some alleviation of heat/desiccation stress (much like inhabiting a microsite), germlings were temporarily physiologically capable of extending their vertical range. In contrast, shade often decreased survival in the low shore. This was probably due to interspecific competition with ephemeral algae. Ephemeral algal growth was enhanced in the low shore, particularly in shaded treatments, due to moist conditions. Reduced survival of germlings due to interspecific competition with filamentous algae has been demonstrated for the Baltic Sea fucoids *Fucus vesiculosus* and *F. serratus* (Berger et al. 2003, Isaeus et al. 2004), and diatoms have been shown to have negative effects on growth and survival of *F. spiralis* (Schonbeck & Norton 1979). Filamentous algae and diatoms overgrow slow-growing fucoids, reducing light levels and depleting nutrients. They can also enhance sediment accumulation, which can have negative effects on germling algae (Berger et al. 2003, Eriksson & Johansson 2003, Isaeus et al. 2004, Schiel et al. 2006).

In Oregon there was a much weaker effect of shore height on survival, and relatively good survival in the high shore. The exception was the summer *F. gardneri* experiment, in which all non-shaded germlings died in the high and mid shores within 1 week. Shade had an overwhelming effect, enhancing survival at all shore heights. Over all experiments, shade had a positive effect on survival in the high shore and in the mid and low shore during warm conditions by reducing heat/desiccation stress, but decreased survival in the low shore in cool conditions. This decrease in survival in the low shore was probably due to competition with ephemerals, similar to the New Zealand species. After one month in autumn experiments, ephemeral algal growth was dense in all low shore fenced treatments, and survival was poor. Survival of *F. gardneri* was better in high and mid shores, and survival of *P. limitata* was limited almost exclusively to the high shore. A few germlings remained in non-shaded treatments in the mid shore at one site. There was little effect of shore height or shade on growth of *F. gardneri*, but *P. limitata* had faster growth in the high shore in spring after 2 weeks, and in autumn after 2 months.

Oregon experiments with improved survival and faster growth in the high shore are in contrast results of New Zealand experiments, and contradict the generalisation that survival and growth should be enhanced in the low shore due to reduced physical stress in a more benign environment. Only a few studies have reported improved survival and growth at higher shore heights. For example, Karez and Chapman (1998) transplanted germlings of three *Fucus* species on the North Sea coastline. *F. spiralis* and *F. vesiculosus* growth and

survival was worst in the lowermost shore height. Also, the high shore alga *Pelvetia canaliculata* has been shown to grow best at higher shore levels, and often decayed if kept submerged (Schonbeck & Norton 1980b, Rugg & Norton 1987). Germlings transplanted into the low shore in Oregon were often very dark, especially during cooler seasons and under shade treatments. Presumably, lower light levels caused a reduction in photosynthesis, and combined with increased interspecific competition with ephemerals, resulted in poor growth and survival.

Oregon species were often subjected to much longer emersion times and higher temperatures in the high shore compared to New Zealand species. Despite this they had relatively good survival and growth. Even at this early post-settlement stage, Oregon germlings appear to be particularly well-adapted to coping with heat/desiccation stress. Evidence that higher shore species are better-adapted to coping with increased emersion and heat stress than low shore species is long standing (Baker 1909, 1910, Zaneveld 1937, Zaneveld 1969, Dring & Brown 1982, Smith & Berry 1986, Skene 2004 and see reviews by Davison 1991, Davison & Pearson 1996). This may partly explain why Oregon species survive and grow much better in the high shore than New Zealand species. However, the temperate regions of the Southern Hemisphere have far higher UV levels than those of the Northern Hemisphere due to ozone depletion (Brown 1999, McKenzie et al. 2003, Lamare et al. 2004). Since UV radiation can have lethal effects and can interact with temperature (Altamirano et al. 2003, Hoffman et al. 2003), this may be an important hemispheric difference influencing fucoid survival in New Zealand and Oregon.

***Grazing***

In general, grazing had strong effects on New Zealand species in the low shore, and in the mid shore during cooler weather. However, grazing had little effect in the high shore and in the mid shore during warmer weather because desiccation and heat stress were more important in influencing germling survival. This is in agreement with the paradigm that grazing is an important structural force in the low shore, and physical stress is important in the high shore (Connell 1972).

Grazing effects were generally weaker and more variable in Oregon experiments. Grazing effects were evident in low shore summer *F. gardneri*, and autumn *P. limitata* experiments. Grazing also had an effect in the mid shore on autumn *F. gardneri*, and in the high and mid shores on spring *P. limitata*. Grazing can be temporally and spatially variable due to the type, abundance and size of grazer and algae (Lubchenco 1978, Underwood & Jernakoff 1981, Lubchenco 1983, Underwood & Jernakoff 1984, Barker & Chapman 1990, Chapman & Johnson 1990, Cervin & Aberg 1997, Lotze & Worm 2000, Lotze et al. 2000,

Jenkins et al. 2005). For example, variable effects of grazing have been shown for the fucoid *Ascophyllum nodosum*. Weak or no grazing effects were found in Sweden (Cervin & Aberg 1997) and in Maine (Dudgeon & Petraitis 2005). However, also in Sweden, Viejo *et al.* (1999) found that there was an interaction effect of grazing with the age of algae and presence of an adult canopy. They found no effect of littorinid grazing on 5 day old germlings under an adult canopy, but in the absence of a canopy, grazing decreased germling survival. After 23 days, grazing was important, independent of other factors. It is interesting to note that the effect of grazing became more important through time, because generally algae escape grazing with an increase in size.

For the species in this study, it is predicted that molluscan grazing would become less effective through time as germlings grew large enough to escape grazing. Laboratory studies showed that when subjected to molluscan grazers, germling survival was enhanced with increase in their size (Dunmore, unpublished data; Schiel, unpublished data). However, as algae reach recruit stage it is possible that they could become vulnerable to other types of grazers, e.g. amphipods, isopods, and fish. The large isopod *Idotea* has been observed feeding on *F. gardneri* recruits (Dunmore, pers. obs.), and fish are known to have large grazing effects on *D. antarctica* recruits (Taylor 2002, Taylor & Schiel 2005). It is clear grazing is temporally and spatially variable and interactions can be highly age- and/or species–specific.

Molluscan grazers were more abundant in Oregon than in New Zealand. It was expected that grazing would have a stronger influence on germling survival in Oregon. Despite low grazer numbers in New Zealand, grazers were large and effectively grazed any plates that were accessible. Grazer numbers may also have been underestimated, because quadrat samples were only taken in the immediate experimental area on flat surfaces, and grazers inhabiting cracks and crevices nearby may have had significant effects. In Oregon, despite their high abundance, grazers did not appear to be as effective in consuming germlings, leading to non-significant treatment effects. Grazers were much smaller, and may not have accessed experimental plates as quickly as New Zealand species. A laboratory experiment showed that limpets and littorines could consume germlings, but rates were slow (Dunmore, unpublished data). After one week of continuous exposure to grazing, survival was still around 50%. It is expected that in field conditions, this grazing rate would be further reduced by a decrease in available grazing time due to duration of low tide and adverse hydrodynamic conditions.

***Ephemeral Algal Growth and Sedimentation***

Ephemeral algae were present in all seasons except summer, when conditions were probably too harsh for their survival. They thrived when conditions were damp and cool, for example in

low shore areas and in shaded treatments. Initially, ephemerals may have had positive effects on germling survival by reducing heat/desiccation stress, but ultimately overgrew and smothered most germlings. Fast growth is essential for germlings to compete successfully with ephemeral algae. *H. banksii*, *F. gardneri* and *P. limitata* generally have very slow growth. *H. banksii* growth was particularly slow during cool months when competition with ephemerals was high. In contrast, *D. antarctica* has much faster growth, with approximately 5x the growth rate of *H. banksii* after 2 months. This difference is partially due to the morphology of the germlings. *H. banksii*, *F. gardneri* and *P. limitata* have bulbous shapes that are well-adapted for resisting desiccation (Brawley & Johnson 1991), but growth is slow. *D. antarctica* germlings have a flat, bladed shape and growth is consequently faster, allowing *D. antarctica* to grow quickly above low-lying ephemerals on the low shore.

Grazers may have positive indirect effects on germling survival by reducing ephemeral algae, thereby decreasing competition. Positive effects of grazing were shown in the Baltic Sea, where selective grazing by littorines on annual species like *Enteromorpha* increased recruitment of *F. vesiculosus* (Worm et al. 1999, Worm et al. 2001). Similar results were found in the New England mid- (Lubchenco 1983) and low-shore (Lubchenco 1978, Lubchenco & Menge 1978), where littorine grazing accelerated succession by reducing competitively superior ephemerals, thereby allowing *F. vesiculosus* and the red alga *Chrondrus crispus* to grow in the mid and low shores, respectively. In experiments in British Columbia, Canada, Kim (1997) also found a positive indirect effect of grazing on *F. gardneri* and *P. limitata*; limpets accelerated succession by consuming ephemerals. For New Zealand and Oregon, a positive grazing effect would be dependent on microsite heterogeneity (for example the presence of cracks, crevices or barnacles) and/or a low abundance or low activity level of grazers to allow germlings to escape, while ephemerals were removed.

In this study, sediments accumulated only in *H. banksii* experiments. Sediment cover was higher in fenced treatments, because sediment was effectively 'bulldozed' by grazers in treatments that had grazer access. After 1 month plates still had only relatively thin covers of sediment, with a maximum of 2mm depth. This level of sedimentation can have positive effects on germling survival, by reducing heat/desiccation stress (Schiel et al. 2006). However, sediments can smother germlings and they often turn anoxic where accumulations are thicker (Chapman & Fletcher 2002, Berger et al. 2003, Isaeus et al. 2004, Schiel et al. 2006). Since sediment accumulation can be heavy in more sheltered areas, it is expected that sediments would have a greater influence on germling survival at such sites.

***Recruitment windows, microsites and unexplained mortality***

Recruitment is a function of settlement in an appropriate habitat and escape from the negative effects of physical and biological pressures. 'Recruitment windows' can be very narrow, as environmental conditions can be highly variable temporally and spatially. Environmental conditions at settlement are particularly important because germling algae are at their most vulnerable in the first few days of post-settlement, and their tolerance to physical stress increases as they age (Bird & McLachlan 1974, Brawley & Johnson 1991, Davison et al. 1993). Survival is enhanced if settlement occurs with the coincidence of benign weather, and/or if settlement is in a suitable microhabitat which provides a refuge from desiccation and thermal stress (Brawley & Johnson 1991, Davison et al. 1993, Johnson & Brawley 1998, Dudgeon & Petraitis 2005), and from grazing activity (Lubchenco 1983, Farrell 1991).

Experiments in this study have shown that outplanting germlings during hot, dry conditions resulted in high mortality within a few days (cf. *H. banksii* and *F. gardneri* summer experiments), but outplanting germlings in more benign conditions resulted in better survival (cf. *H. banksii* and *F. gardneri* autumn experiments). Stochastic weather events such as extremely hot and dry weather, combined with low tides of long duration have been shown to hugely affect recruitment and adult survival (Schonbeck & Norton 1978, Hay 1979). Settlement at such times is unlikely to result in successful recruitment.

Although survival may be higher when settllement is in cooler seasons, other factors impact on recruitment. Slower growth exposes germlings to grazing and competition for longer periods. *H. banksii* reproduces year-round, but recruitment is almost exclusively the result of settlement in spring and early summer (Schiel 2006). The present study has shown that after one month in the low shore, summer *H. banksii* grew 4x as large as autumn germlings. Presumably, in cooler months slow growth rates of germlings led to high mortality due to grazing and competitive interactions, resulting in low recruitment. *D. antarctica* reproduces in late autumn to early spring, which reduces germling mortality due to heat/desiccation stress. However, *D. antarctica* has a much higher growth rate than other fucoids examined in this study, which enables it to successfully escape grazing and compete with ephemerals in cooler months.

Microsites are highly important in influencing germling survival. Cracks and crevices, barnacles, canopy and turfing algae have been found to have large effects on germling survival. In North America, the barnacle-grazer-fucoid relationship has received particular attention. Studies attempting to evaluate the effect of barnacles on fucoid germling survival have found positive effects due to reduced grazing and desiccation (Lubchenco 1983, Farrell 1991, Kim 1997, van Tamelen & Stekoll 1997). The relative effects were variable between

studies, possibly due to site differences (Kim 1997, van Tamelen & Stekoll 1997). For example, herbivory was relatively unimportant at a site in Alaska, but barnacles reduced heat and desiccation stress (van Tamelen & Stekoll 1997). In contrast, barnacles reduced grazing at sites in Oregon (Farrell 1991). Effects of barnacles appear to be highly temporally and spatially variable. At our sites in Oregon, barnacles are expected to reduce heat and desiccation stress during hot and dry conditions and enhance survival during times of strong grazing effects.

In addition to molluscan grazing and desiccation/heat stress, a multitude of other factors influence germling survival. Experiments in this study often had high unexplained mortality. For example, in many Oregon experiments grazing and heat/desiccation effects were relatively low but germling mortality still occurred across all shore heights and treatments. This could have been due to effects of wave action, or possibly micrograzers. Gammarid amphipods, and tiny limpets and littorines (<2mm) were often present and had access to all treatments because they could move through the fence mesh. Gammarid amphipods have been shown to graze algal germlings (Parker & Chapman 1994, Cervin & Aberg 1997, Viejo et al. 1999), and may have contributed to the unexplained mortality. It is unlikely that the tiny gastropods were capable of causing significant mortality, since their larger counterparts rarely had much effect.

***Summary***

This study illustrates the great amount of variation in early life stage demographies between species. Responses to physical and biological stresses can be highly species specific and this has important ramifications for ecologists using model organisms to define community structure and interactions. It is essential to have information on fine scale differences in species reproduction, dispersal and early life histories because these characteristics can have profound effects on their adult distributions, abundances and ecological interactions. In addition, the variation exhibited between seasons and sites highlights the need for experiments to be conducted at different times and at multiple sites because temporal and spatial changes in physical (e.g. temperature, wave climate) and biological conditions (e.g. grazer numbers, inter- and intraspecific competition) can have large influences on experimental results.

In New Zealand, *H. banksii* and *D. antarctica* have upper limits that are ultimately determined by heat and desiccation stress. During cooler conditions, upper limits may temporarily be extended but heat and desiccation eventually cause mortality. Low shore limits are primarily determined by a combination of grazing and competition with ephemeral algae. These interactions are influenced by growth rate, which is highly variable between species and season.

Shore height did not have such a strong effects survival of Oregon species as it did on New Zealand species, unless climatic conditions were severe. *P. limitata* survived and grew poorly on the low shore. Poor physiological performance, in combination with grazing and competition probably limit its distribution to the high shore. *F. gardneri* does inhabit the low intertidal, but is much more abundant in the high shore. Its abundance is probably limited by similar factors that control the distribution of *P. limitata*. In addition, dispersal of these algae is likely to be highly localised (van Tamelen et al. 1997 Chapter 3, see review by Chapman 1995), and this would also restrict their ability to settle and recruit in abundance in other areas. Settling in the low shore during cooler seasons may also lead to poor recruitment. The experiments in this study were done during relatively warm conditions, and survival in the low shore was good. During cooler seasons the conditions in the low shore are more adverse to germling survival because low tides occur at night, wave forces are stronger, and light and temperature levels are lower. Lower light and temperature levels would lead to poorer growth and longer exposure to grazing. Germlings settled in the high shore may have an advantage that enables them to endure the winter.

The effect of increasing physiological stress is important in the context of climate change. Species inhabiting the intertidal zone may be the worst affected because they have to cope with extreme environmental fluctuations, and vulnerable early life stages may be particularly susceptible to any increases in these stresses. On a regional scale, sub-lethal and lethal effects of heat/desiccation stress may be stronger on species near their warmer latitudinal limits, and ranges may be extended at cooler latitudinal limits.

# Chapter 5
# General Discussion

***Summary***

This study tested hypotheses about differences in the early life histories and demographies of several species of fucoid algae. The underlying premise was that fine-scale differences in dispersal, settlement and early life stage survival and growth are variable between species and across small temporal and spatial scales, and this produces large-scale variations in recruitment. An important aspect of this study was the repetition of experiments through time at different sites. Dispersal, settlement and early life stage survival were highly variable, and variation within species at different times often matched the variation between species. The repetition of experiments is important because many experiments are only conducted over short time frames, at single sites, and results may not be typical of other areas or times, especially for species with long reproductive periods. The variability in results found in this study highlights the value of experiments being done over several relevant spatial scales under a range of conditions.

Results showed that both positive and negative effects had important influences on dispersal, settlement and early life stage survival and this is thought to contribute to the high amount of variation in results over small temporal and spatial scales. Observed effects from this study, and other factors considered to be important are summarized in Table 5.1. Positive effects of interactions have received increasing attention recently (Bertness & Leonard 1997, Bertness et al. 1999, Stachowicz 2001, Bertness et al. 2002, Bruno et al. 2003, Lilley & Schiel 2006). Clearly, a complex interplay of positive and negative interactions is important in influencing the early life stages of algae.

The use of artificial plates was instrumental in this study. The early life stages of algae are difficult to study due to their microscopic size and the plates used provided a standard substrate that had similar micro-topographical and temperature retention properties of the natural rock, while still allowing observation of the germlings. A pilot experiment showed they were a superior settlement surface for fucoid seaweed than concrete, and they have since been used in numerous experiments examining the early life stages of algae (Taylor 2002, Taylor & Schiel 2003, Schiel et al. 2006).

**Table 5.1** Summary of factors with positive and negative effects on the dispersal, settlement and early life stages of fucoid algae. Bold indicates observed effects in this study. Negative effects decrease dispersal, settlement densities and early life stage survival and growth. Positive effects increase or enhance the same processes or stages.

| Process/Stage | Factor | Negative effects | Positive effects |
|---|---|---|---|
| Dispersal | Egg size | **Large size – increases sinking rate** | **Small size – decreases sinking rate** |
| | Mucilage | Aids adherence to substrate<br>**Carries propagules to substrate** | **Aids in buoyancy** |
| | Substratum | Heterogenous – traps, aids adherence | Smooth – adherence difficult |
| | Wave action, currents | Introduces propagules to substrate quickly | Increases resuspension |
| | Canopy | Reduces water flow, increasing settlement | Increases resuspension. |
| Settlement | Canopy | Sweeps propagules, barrier to settlement | **Reduces water flow, increasing settlement** |
| | Turfs | Preemptive exclusion | Traps propagules |
| | Substratum | Smooth – adherence difficult | Heterogenous – traps, aids adherence |
| Early Life Stage | Grazing | **Large direct source of mortality** | **Indirect effect – reduces ephemerals, moves sediment** |
| | Heat/desiccation | **Large direct source of mortality** | **Reduces ephemerals** |
| | Ephemerals | **Interspecific competition** | **Reduces heat/desiccation** |
| | Sediment | **Smothers, scours, reduces light** | **Reduces heat/desiccation** |
| | Density | Intraspecific competition | Swamps areas – increases grazing escapes<br>Reduces heat/desiccation |
| | Canopy | Sweeps germlings<br>Reduces light<br>Reduces heat/desiccation – increases grazer activity | Reduces heat/desiccation |
| | Turfs | Enhances sediments<br>Increased grazing | Reduces heat/desiccation<br>Reduces grazing |
| | Wave action | Detachment<br>Increases scour | Removes sediment |

***Variation in settlement***

Rocky intertidal communities are characterized by patchy mosaics of bare space, algae and sessile and mobile invertebrates. To understand the causes of patchiness in intertidal algal communities, settlement patterns of *H. banksii* and *Cystophora* spp. were examined for over three years at a semi-exposed site in New Zealand. It was hypothesized that settlement would

be highly variable between shore heights and habitats, and that bare patches were caused by a lack of propagule supply (Table 5.2 A, B). Although settlement proved to be highly variable between shore heights and habitats, bare patches had some settlers but densities were reduced. It was concluded that the patches were not caused by a lack of supply, but that post-settlement mortality was more important in setting recruitment patterns. Grazing on the smooth, bare rock, and high heat/desiccation stress causes mortality of newly settled propagules. Settlement was disproportionately high under adult canopies, but recruitment rarely occurs there (Lilley & Schiel 2006 Dunmore, unpublished data). This is similar to results found in California for *Pelvetia* (=*Silvetia*) *compressa* (Johnson & Brawley 1998). Settlement was 1-2 orders of magnitude greater under canopies than immediately outside them, but few juveniles were found there. The *H. banksii* understorey consists mainly of coralline turfs that appear to be unsuitable for fucoid recruitment. It appeared that fucoid zygotes could not attach well to the fronds of corallines. When they did attach, and grow, they were lost as coralline frond broke away. Even when thick turfs are removed, little recruitment occurs on bare rock or on encrusting corallines under a canopy (Dunmore, unpublished data). Canopies can remove germlings by sweeping, enhance numbers and activity of grazers, or reduce light levels (Johnson & Brawley 1998). In addition, turfs hold sediment, and germlings attach poorly in sedimented conditions (Schiel *et al.* 2006).

The results from Chapter 2 indicated that dispersal was limited, with disproportionately higher settlement directly under adult plants. Prior to this study, little information was available on dispersal and settlement numbers with increasing distances from populations.

**Table 5.2** Hypotheses tested in each chapter.

| Chapter | Hypothesis | Accept | Reject |
|---|---|---|---|
| 2 - Settlement | A) Settlement of *H. banksii* and *C. torulosa* is variable among tidal heights and habitats | ✓ | |
| | B) Bare patches within *H. banksii* habitats are caused by a lack of supply | | ✓ |
| 3 - Dispersal | C) Egg sizes affect sinking rates | ✓ | |
| | D) Dispersal is highly localized for all species | | ✓ |
| | E) An exponential decline in settlement densities would always occur with increasing distance from the source | | ✓ |
| 4 – Early life stage survival and growth | F) Survival and growth differs across shore heights | ✓ | |
| | G) Grazing has unequal effects across shore heights | ✓ | |
| | H) Provision of shade would affect growth and survival across shore heights | ✓ | |

***Dispersal***

Many factors influence algal dispersal, including propagule characteristics and behaviour, height of gamete release above the substratum, the density of adult plants, substrate type, topography and hydrodynamic conditions (see reviews Hoffmann 1987, Santelices 1990, Fletcher & Callow 1992, see reviews Norton 1992, Schiel & Foster 2006). In my study, size of eggs and the presence of mucilage appeared to have large effects on dispersal. The hypothesis that larger eggs would sink faster was accepted (Table 5.2 C). This has been found for many species (Coon *et al.* 1972, Okuda & Neushul 1981, Hoffmann & Camus 1989), and slower sinking eggs are thought to spend a longer time in the water column and have greater dispersal. This was true for the species studied here; *Durvillaea* spp. had the smallest eggs and the longest dispersal. Species with larger eggs had more restricted dispersal.

Mucilage had positive and negative influences on dispersal distances. Positive effects were observed in *Durvillaea* spp. because the mucilage appeared to be buoyant, and eggs descended out of the mucilage that floated on the surface water. *F. gardneri* eggs were released in much larger amounts of more viscous mucilage, and this mucilage often transported eggs to the understorey. This would reduce dispersal because fertilization and attachment may occur before immersion by the incoming tide (Brawley & Johnson 1992, Brawley *et al.* 1999), and water motion is reduced in algal canopy areas (Santelices 1990).

Dispersal was much further than expected for *Durvillaea* spp., which had settlement 32 m from the source. Therefore the hypothesis that all species would have highly localized dispersal was rejected (Table 5.2 D). The other species examined had much more restricted dispersal, with very low densities further than 0.5 m from the source. The hypothesis that there would always be an exponential decline in densities with distance from the source for all species was rejected because although this occurred in general, it was not always the case (Table 5.2 E). During periods of high settlement densities, sharp declines in densities were observed with increasing distance from the source. Sampling times with low settlement densities had very little difference in densities with distance.

Low dispersal distances are typical for fucoids due to their large, negatively buoyant eggs. In addition, some species have been shown to release gametes only during periods of calm water (Serrao *et al.* 1996, Pearson & Brawley 1998). If this is general for all fucoids, it would also explain their low dispersal of propagules. Further examination of the environmental conditions during gamete release in more species is needed to further our knowledge of fine-scale temporal variation in gamete release and how this affects dispersal.

Despite the short-range dispersal of propagules, long-range dispersal is possible via the detachment and drifting of adult plants, and release at a distant site. However, this method

is considered highly episodic and may not be very effective for most species (van den Hoek 1987). Most algae end up as beach cast, high on the shore and even if fertilisation is successful, dispersal to a suitable habitat may not be. This is of particular relevance for low shore species. In addition, dioecious species would also need to have male and female plants in fairly close proximity to ensure fertilisation.

For all species, settlement densities declined with distance from source populations, and this may have large ramifications for recruitment. Positive effects of germling density on recruitment have been observed in several fucoid species due to reductions in heat/desiccation stress and grazing (Hruby & Norton 1979, Ang & DeWreede 1992). Density has also been shown to be important in recruitment of *H. banksii*. A minimum of 250 -750 settlers per $cm^2$ is needed to produce >1 recruit per $cm^2$, which is required to produce a closed canopy (Schiel 2004). A closed canopy has important effects on the understorey community by increasing taxa richness and species abundances (Lilley 2004).

This study is important because it examined the densities of germling settlement with increasing distance from source populations to investigate dispersal. Most studies have inferred dispersal distances from recruitment data, and this can underestimate dispersal considerably. For example, if dispersal of *D. antarctica* was estimated by examining the distance of recruits from populations, estimates would be very low because recruitment is generally only successful close to populations.

***Interaction of settlement variation with early life stage survival and growth***

Hypotheses that the survival and growth of germlings would differ across species, seasons and tidal heights were accepted because survival and growth was highly variable across all of these factors (Table 5.2 F). In agreement with other studies of fucoids and algae in general, mortality of early life stages was high. Rates of mortality differed across species, and across the conditions experienced. In New Zealand, germlings that settle at mid and high shore heights had very poor survival, but Oregon species had similar survival at all shore heights. Even at the microscopic stage, germlings have intrinsic responses to the biological and physical environment which ultimately determine their adult distributions and abundances.

Heat/desiccation stress was an important source of mortality for New Zealand species during all experiments. Massive mortality occurred in the high shore in only a few days. However, Oregon species dealt with heat/dessication very well. Germlings appeared to dry out and had shriveled appearances, but recovery was very good after re-immersion. Ultimately, high shore germlings often survived better than low shore germlings which

contradicts the paradigm that growth and survival on the low shore should be enhanced due to reduced physical stress.

The effect of season was strong; experiments in cooler conditions had better survival, but in New Zealand growth was much slower. There is an important trade-off for reproducing and settling at different times of the year; settlement in cooler seasons exposes germlings to less heat/desiccation stress, but slower growth exposes them to competition and grazing for longer periods. This is particularly relevant for species reproducing year-round. *H. banksii* settles throughout the year, but nearly all recruitment occurs during spring – early summer (Lilley & Schiel 2006). Growth of this species in autumn and winter is very slow and makes them susceptible to grazing. In contrast, *D. antarctica* reproduces only during cooler months, reducing germling mortality due to heat/desiccation stress. Settlement densities are much higher than the other species examined in this study which swamps areas with germlings. In addition, their growth is much faster, allowing them to escape molluscan grazing.

Many studies have identified grazing as an important source of mortality, but there have also been positive or no effects reported (Lubchenco 1978, Lubchenco & Menge 1978, Chapman & Johnson 1990, Cervin & Aberg 1997, Dudgeon & Petraitis 2005). In this study, grazing was important at some stage at all sites and shore levels, but was temporally and spatially variable (Table 5.1 G). Overall, grazing was stronger lower on the shore because heat/desiccation was more important in the high and mid shores. Grazers were not more abundant on the low shore, but they had more time for foraging. Preventing grazer access from plates with fences improved survival, but then ephemeral algal growth was enhanced. Competition with ephemeral algae clearly was an important interaction for species with very slow growth like *H. banksii*, *F. gardneri* and *P. limitata*, which were overgrown and smothered. *D. antarctica* has faster growth (even in cooler months) and this may be an important difference that enables it to successfully recruit to the low shore.

Grazers were more effective at removing germlings in New Zealand than Oregon. This was despite Oregon having higher abundances of grazers. New Zealand grazers may be more effective because of their larger sizes. There were also a more diverse range of species with different feeding mechanisms (Steneck & Watling 1982) which may have contributed to their stronger effects.

***Disturbances***

Marine ecosystems are vulnerable to human mediated and environmental disturbances, and examination of their recovery has received much attention. The recovery of habitat forming algae is of particular interest because of their important roles in structuring

communities. The recovery of fucoid algal habitats following large-scale disturbances has been examined after oil spills (van Tamelen *et al.* 1997, Stekoll & Deysher 2000, Driskell *et al.* 2001), urban pollution (Benedetti-Cecchi *et al.* 2001)**,** trampling (Povey 1991, Keough & Quinn 1998, Schiel & Taylor 1999), environmental events of storms (Underwood 1998, Underwood 1999) and ice scour (McCook & Chapman 1997). Their recovery is generally very slow, delayed by their slow growth and short dispersal. For example, Underwood (1998, 1999) found extremely slow recovery rates of *H. banksii* after a severe storm in Australia. Recovery could take up to 5 years, depending upon the severity of the disturbance.

Results from this study suggest recovery from large scale disturbances could be constrained by dispersal. *H. banksii*,*C. torulosa* and *F. gardneri* had very low settlement densities at distances over 0.5 m from the source, and this may severely limit their ability to re-colonize areas. *Durvillaea* spp. had much higher settlement densities further from source plants and it is expected that their ability to re-colonize would not be as limited. Timing of disturbance would also be a large factor in recovery; for species reproducing year-round, disturbances in cooler months would take longer to recover due to slow growth rates, and recruitment may not occur until peak reproductive periods. For *Durvillaea* spp., disturbances in spring would not begin to have recruitment until the following winter.

***Conclusions***

Fucoid algae are generally long-lived as adults, mostly in the order of 7-10 years, so plants that are well-established have numerous opportunities for reproduction over their life-times. However, all of the New Zealand species, except *Durvillaea*, become reproductively active within a year of settlement. Because of their limited reproductive output, they have a much diminished chance of settlement success compared to other plants. It is likely that most settlers come from established adult stands. The high densities of plants in these stands, and their extensive coverage of the intertidal zone in some areas, gives them a huge reproductive potential. Small-scale disturbances from a wide range of natural and anthropogenic sources are settled relatively quickly because most eggs fall near adult canopies. Even though disturbances may take a few years to recover (Underwood 1998, Underwood 1999, Lilley & Schiel 2006, Schiel 2006), there is a still a high probability that they will eventually recover. The premium on these life histories of most species, therefore, seems to be maintenance. Settling in the parental environment gives the greatest probability of success, particularly in highly disturbed shallow coast environments.

The vagaries of disturbances and the heterogeneity of both physical and biotic environments provide mostly unpredictable opportunities for these species, most of which

reproduce year-round. All of the species are widely distributed geographically, however, so the constraints on settlement and growth experienced in Southern New Zealand or Central Oregon may not be the same throughout the ranges of these species. For example, it is plausible that *H. banksii* originated in Australia, where it is warmer, grazers are different and there are significant differences in its demography than in New Zealand (Schiel 2004). Understanding these species, therefore, is different to understanding how they operate in specific conditions and in particular species assemblages. Species at their latitudinal limits may have severe constraints on their growth and reproduction. This is important when considering changes to communities due to climate change.

In Southern New Zealand, all of these fucoids are linked to the varying sources of distributions across the tidal gradient. In many ways, species such as *H. banksii* are poorly adapted. Year-round reproduction is highly ineffectual, and effort would be much more likely to succeed if concentrated in the spring and early summer. Nevertheless, *H. banksii* is the only large alga that can survive throughout the upper mid-intertidal zone, so its dominance is unchallenged by other fucoids. In Oregon, however, several species of barnacles, mussels, red and green algae may effectively compete with fucoids for space.

Overall, the fine-scale interactions of the early life stages of these species determine adult distributions. This thesis has delineated and quantified the constraints imposed on these species by their environments, and also by their innate life history constraints of all species other than *Durvillaea* in quickly colonizing more distant sites. The most important interactions are with the physical environment, grazers and understorey algae on early life stages, rather than adult interactions. It is increasingly clear that understanding the effects on early life stages is the key to understanding the distributions and abundance patterns of these major habitats.

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# Appendices

**Appendix I.** Summary tables and graphs of species from quadrat sampling of habitats in the early life stage survival experiments (Chapter 4).

**Table 1.** Dominant organisms at each tidal height at each site in sheltered habitats (*H. banksii* experiments) in Kaikoura, New Zealand. Data are percent covers of algae and sessile invertebrates, and numbers of mobile invertebrates in 0.25m$^2$ quadrats. *n*=5.

| Group | Species | First Bay | | | Seal Reef | | |
|---|---|---|---|---|---|---|---|
| | | High | Mid | Low | High | Mid | Low |
| Grazers | Littorines (*Austrolittorina antipodum* and *A. cincta*) | 0 | 0 | 0 | 107 | 0 | 0 |
| | *Cellana denticulata* | 13 | 6 | 0 | 2 | 8 | 0.4 |
| | *Cellana flava* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Cellana ornata* | 0 | 0.2 | 0 | 3 | 0.2 | 0 |
| | *Cellana radians* | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Siphonaria australis* | 2 | 9 | 3 | 0 | 20 | 16 |
| | *Notoacmea sp.* | 0.2 | 1 | 0 | 0.4 | 1 | 0 |
| | *Patelloida corticata* | 0 | 0.2 | 0 | 0 | 5 | 0.2 |
| | *Sypharochiton pelliserpentis* | 0 | 1 | 0 | 0 | 3 | 1 |
| | *Onchidella* sp. | 0 | 0 | 0 | 0 | 0.2 | 0 |
| | *Melagraphia aethiops* | 2 | 2 | 0 | 0.2 | 0 | 1 |
| | *Turbo smaragdus* | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Rissolopsis varia* | 2 | 0 | 0 | 1 | 6 | 0.4 |
| Predators | *Haustrum haustorium* | 0.2 | 0.4 | 0 | 0 | 1 | 0.2 |
| | *Haustrum scobina* | 0 | 0 | 0 | 0 | 0 | 0 |
| Sessile invertebrates | *Anthopleura* sp. | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Isactinia olivacea* | 0 | 0.4 | 0 | 0 | 0 | 0 |
| | *Aulacomnya ater maoriana* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Xenostrobus pulex* | 0 | 0 | 0 | 1 | 0 | 0 |
| | *Chamaesipho* spp. | 0 | 0 | 0 | 3 | 0 | 0 |
| | *Epopella plicata* | 0 | 0 | 0 | 1 | 0 | 0 |
| Bare | Bare | 98 | 86 | 4 | 96 | 61 | 27 |
| Algae | *Hormosira banksii* | 0 | 2 | 17 | 0 | 6 | 6 |
| | *Durvillaea antarctica* | 0 | 0 | 2 | 0 | 0 | 0 |
| | *Cystophora torulosa* | 0 | 0 | 15 | 0 | 0 | 0 |
| | *Cystophora scalaris* | 0 | 0 | 7 | 0 | 0 | 0 |
| | *Carpophyllum maschalocarpum* | 0 | 0 | 1 | 0 | 0 | 0.4 |
| | *Notheia anomala* | 0 | 0 | 1 | 0 | 0 | 0 |
| | *Halopteris* sp. | 0 | 0 | 3 | 0 | 0 | 1 |
| | *Colpomenia/Leathesia* spp. | 0 | 0.2 | 1 | 0 | 0.4 | 1 |
| | *Adenocystis utricularis* | 0 | 0 | 0 | 0 | 1 | 7 |
| | Encrusting brown | 0 | 1 | 31 | 0 | 0 | 32 |
| | *Scytothamnus australis* | 0 | 0 | 0 | 0.4 | 0 | 0 |
| | Corallines | 0.4 | 12 | 62 | 0 | 36 | 21 |
| | *Ceramium* sp. | 0 | 0 | 0.2 | 0 | 0 | 0 |
| | *Champia* spp. | 0 | 0 | 0.2 | 0 | 0 | 0 |
| | *Gelidium* sp. | 0 | 1 | 0.2 | 0 | 3 | 10 |
| | *Gigartina chapmanii* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Lophothamnion hirtum* | 0 | 0 | 0 | 0 | 2 | 1 |
| | *Polysiphonia* sp. | 0 | 0 | 0 | 0 | 0 | 1 |
| | *Porphyra* sp. | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Ulva* spp. | 0 | 0 | 0.2 | 0 | 1 | 1 |

**Table 2.** Dominant organisms at each tidal height at each site in exposed habitats (*D. antarctica*) in Kaikoura, New Zealand. Data are percent covers of algae and sessile invertebrates, and numbers of mobile invertebrates in 0.25m$^2$ quadrats. *n*=5.

| Group | Species | First Bay | | | Seal Reef | | |
|---|---|---|---|---|---|---|---|
| | | High | Mid | Low | High | Mid | Low |
| Grazers | Littorines (*Austrolittorina antipodum* and *Austrolittorina cincta*) | 148 | 0 | 0 | 193 | 0 | 0 |
| | *Cellana denticulata* | 6 | 9 | 1 | 2 | 10 | 0 |
| | *Cellana flava* | 0.2 | 0 | 0 | 0.2 | 0 | 0 |
| | *Cellana ornata* | 1 | 2 | 0 | 2 | 0 | 0 |
| | *Cellana radians* | 1 | 0.2 | 0 | 0 | 1 | 1 |
| | *Siphonaria australis* | 6 | 1 | 0 | 2 | 5 | 5 |
| | *Notoacmea sp.* | 1 | 7 | 0 | 1 | 0.2 | 2 |
| | *Patelloida corticata* | 0.4 | 0 | 7 | 0.2 | 0 | 20 |
| | *Sypharochiton pelliserpentis* | 0 | 1 | 2 | 0 | 2 | 0 |
| | *Onchidella* sp. | 0 | 1 | 0 | 0 | 0 | 0 |
| | *Melagraphia aethiops* | 0 | 0 | 0 | 0 | 0.2 | 0 |
| | *Turbo smaragdus* | 0 | 0.2 | 0.3 | 0 | 0 | 0 |
| | *Rissolopsis varia* | 0.4 | 0.4 | 0 | 1 | 0.4 | 0 |
| Predators | *Haustrum haustorium* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Haustrum scobina* | 0.4 | 0 | 0 | 0 | 0 | 0 |
| Sessile invertebrates | *Anthopleura* sp. | 0 | 0 | 0 | 0 | 0.2 | 0 |
| | *Isactinia olivacea* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Aulacomnya ater maoriana* | 0 | 0 | 0 | 0 | 1 | 0 |
| | *Xenostrobus pulex* | 0 | 0 | 0 | 0.4 | 0 | 0 |
| | *Chamaesipho* spp. | 0 | 0 | 0 | 5 | 0.2 | 0 |
| | *Epopella plicata* | 0 | 0 | 0 | 7 | 0 | 0 |
| Bare | Bare | 96 | 91 | 40 | 87 | 91 | 7 |
| Algae | *Hormosira banksii* | 0 | 0.2 | 0 | 0 | 1 | 0 |
| | *Durvillaea antarctica* | 0 | 0 | 77 | 0 | 1 | 2 |
| | *Cystophora torulosa* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Cystophora scalaris* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Carpophyllum maschalocarpum* | 0 | 0 | 1 | 0 | 0 | 7 |
| | *Notheia anomala* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Halopteris* sp. | 0 | 0 | 0 | 0 | 0 | 10 |
| | *Colpomenia/Leathesia* spp. | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Adenocystis utricularis* | 0 | 0 | 0 | 0 | 0 | 0 |
| | Encrusting brown | 0 | 0 | 0 | 0.2 | 0.4 | 7 |
| | *Scytothamnus australis* | 0 | 0 | 0 | 0 | 0.2 | 0 |
| | Corallines | 1 | 8 | 55 | 0 | 9 | 61 |
| | *Ceramium* sp. | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Champia* spp. | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Gelidium* sp. | 0.2 | 0.2 | 2 | 0 | 2 | 2 |
| | *Gigartina chapmanii* | 0 | 0 | 0 | 0 | 0 | 7 |
| | *Lophothamnion hirtum* | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Polysiphonia* sp. | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Porphyra* sp. | 0 | 0.4 | 0 | 0 | 0 | 0 |
| | *Ulva* spp. | 0 | 0 | 0 | 0 | 0 | 12 |

**Table 3.** Dominant organisms at each tidal height at each site in Oregon, U.S.A. Data are percent covers of algae and sessile invertebrates, and numbers of mobile invertebrates in 0.25m$^2$ quadrats. *n*=5.

| Group | Species | Depoe Bay | | | Fogarty Creek | | |
|---|---|---|---|---|---|---|---|
| | | High | Mid | Low | High | Mid | Low |
| Grazers | *Lottia* sp. | 73 | 177 | 196 | 73 | 254 | 181 |
| | Littorines | 900 | 272 | 0 | 106 | 257 | 322 |
| Sessile invertebrates | Anemones | 0 | 0 | 0.2 | 1 | 0.8 | 2 |
| | Mussels | 0.6 | 34 | 33 | 19 | 82 | 2 |
| | Barnacles | 69 | 42 | 15 | 8 | 20 | 6 |
| Bare | Bare | 31 | 22 | 10 | 63 | 5 | 4 |
| Algae | *F. gardneri* | 2 | 0 | 0 | 38 | 0.1 | 0 |
| | *P. limitata* | 20 | 0 | 0 | 0.2 | 0 | 0 |
| | *Endocladia muricata* | 2 | 2 | 0.4 | 5 | 2 | 0.8 |
| | Coralline algae | 0 | 0.3 | 33 | 0 | 0 | 0 |
| | *Polysiphonia* sp. | 0 | 2 | 13 | 0 | 0 | 0 |
| | *Mastocarpus papillatus* | 1 | 0.5 | 0.2 | 3 | 0.2 | 0 |
| | *Mazaella parksii* | 0 | 0 | 0 | 4 | 0 | 0 |
| | *Microcladia* sp. | 0 | 0 | 2 | 0 | 0 | 0 |
| | *Neorhodomela larix* | 0 | 0 | 0 | 0 | 0 | 58 |
| | *Odonthalia floccosa* | 0 | 0 | 0 | 0.4 | 0 | 0 |
| | *Ulva* sp. | 0 | 0 | 0 | 0 | 0 | 0.7 |
| Seagrass | *Phylospadix* sp. | 0 | 0 | 4 | 0 | 0 | 0 |

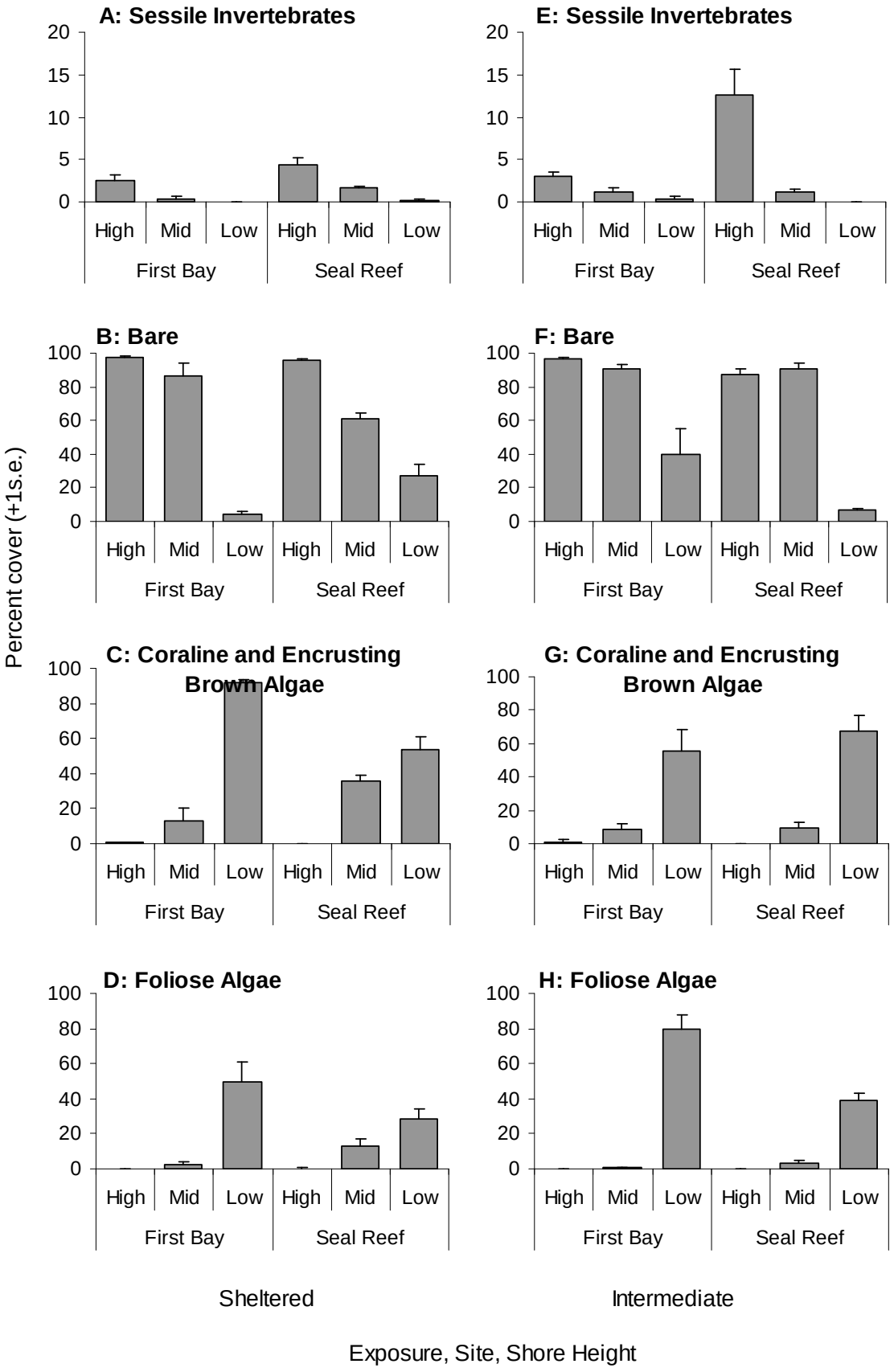


**Figure 1.** Percent covers of Sessile Invertebrates (A, E), Bare (B, F), Turfing and Encrusting Understorey Algae (C, G) and Canopy Algae (D, H) per $0.25m^2$ at each New Zealand site. *n* = 5. See Tables 1 and 2 for details of species.

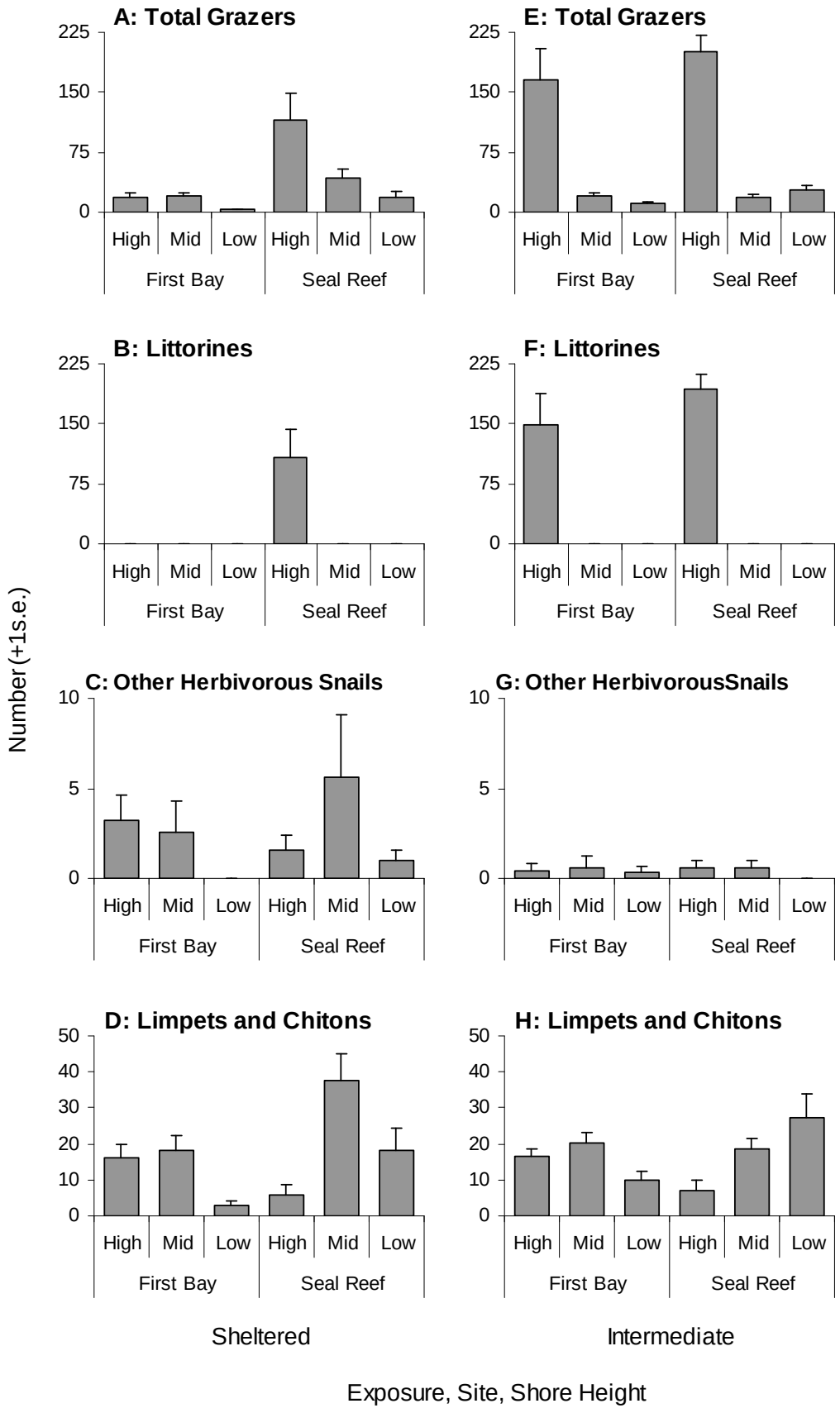


**Figure 2.** Numbers of Total Grazers (A, E), Littorines (B, F), Other Herbivorous Snails (C, G) and Limpets and Chitons (D, H) per 0.25m$^2$ at each New Zealand site. *n* = 5. See Tables 1 and 2 for details of species.

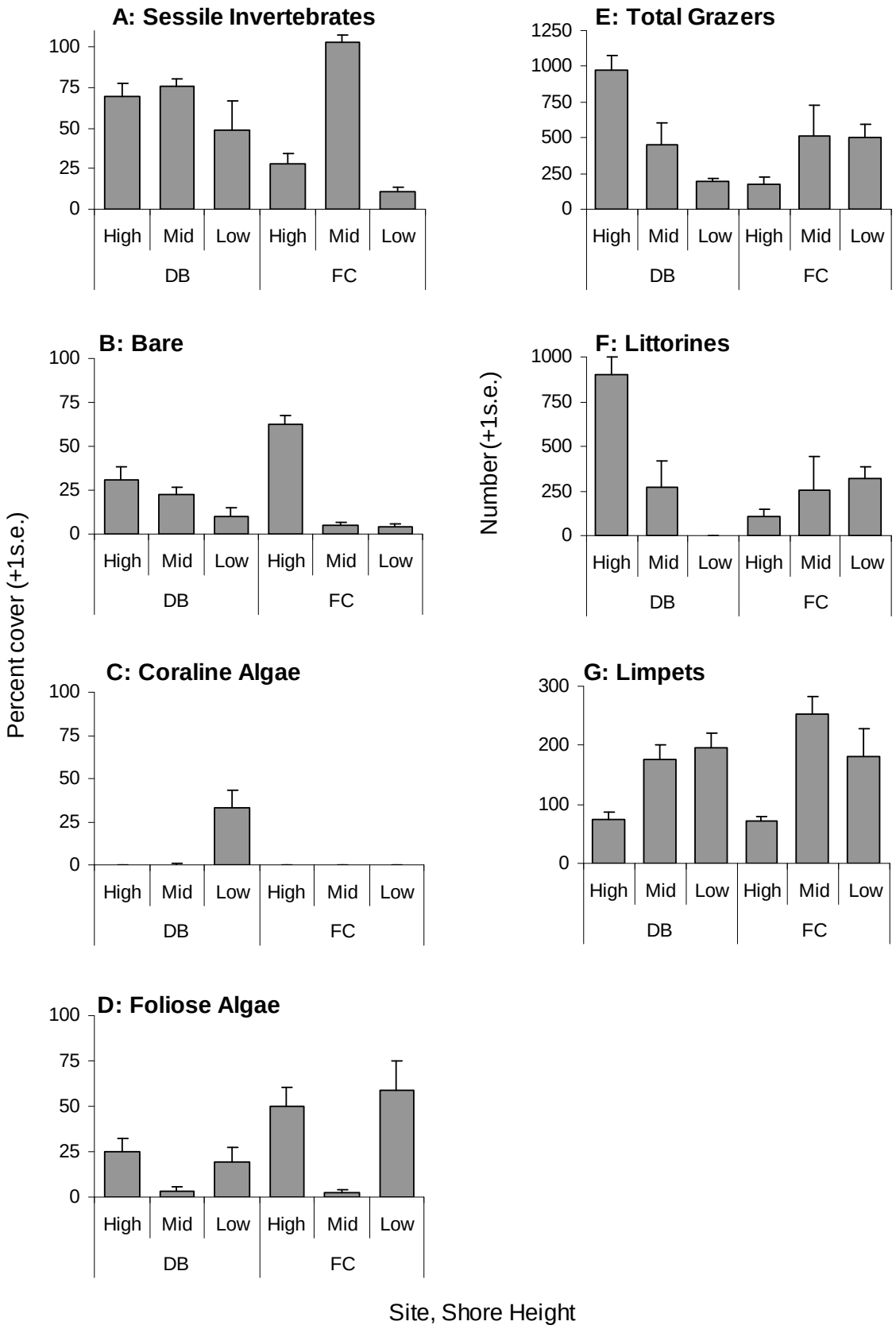


**Figure 3.** Percent covers of Sessile Invertebrates (A), Bare (B), Coraline Algae (C) and Foliose Algae (D), and numbers of Total Grazers (E), Littorines (F), and Limpets (G) per 0.25m$^2$ at each Oregon site. *n* = 5. See Table 3 for details of species.

**Appendix II.** Figure of *H. banksii* germling survival. Germlings were 3 weeks old at the start of the experiment. Illustrates good survival at all shore heights, relative to *H. banksii* summer and autumn, and *D. antarctica* spring experiments, despite temperatures being very high.

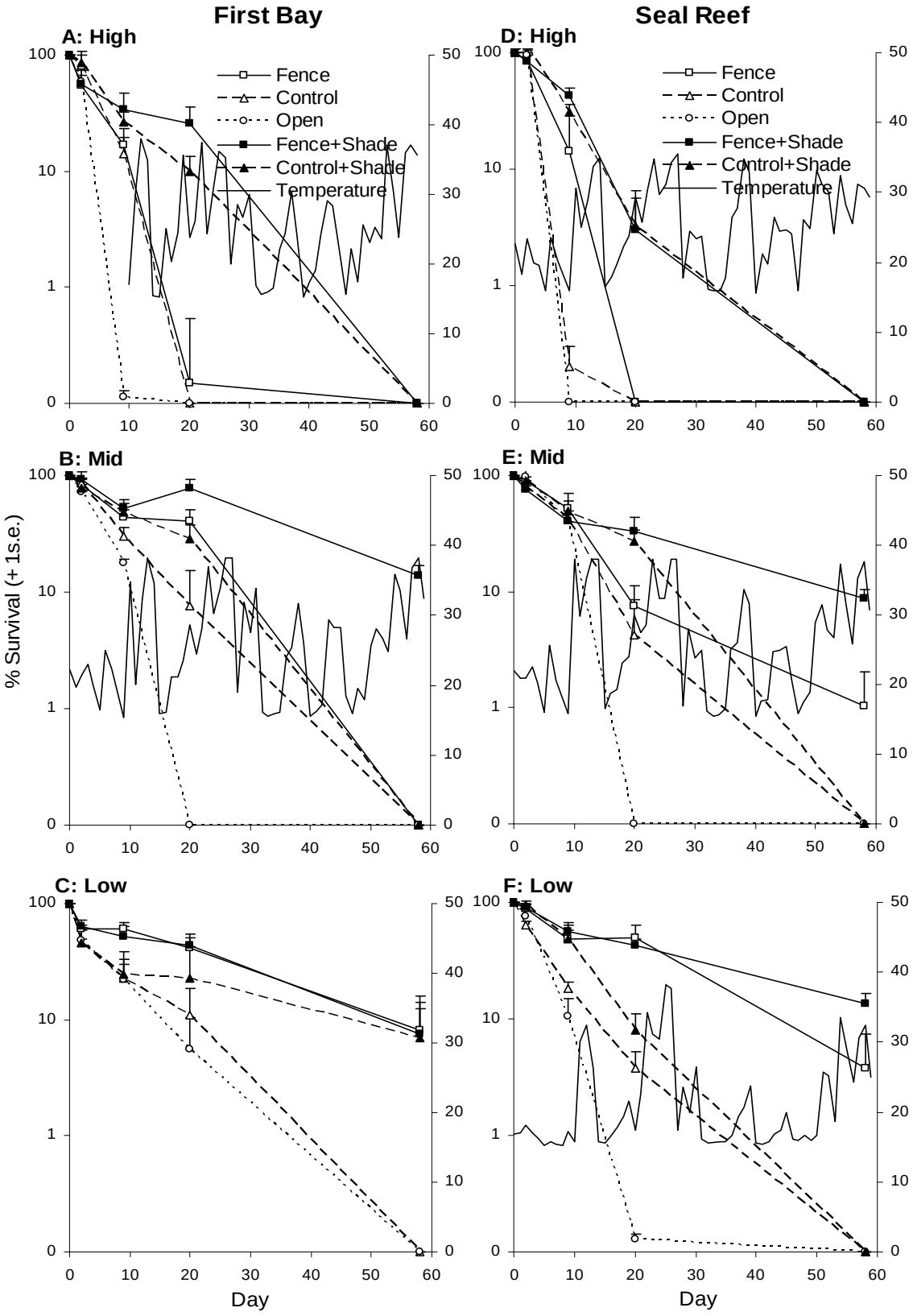


**Figure 4.** Summer, Kaikoura. Percent survival of *H. banksii* germlings transplanted upshore in different grazing and heat stress/desiccation treatments at First Bay (A-C) and Seal Reef (D-F) in summer 2002. Replicates = 3. Maximum daily temperatures are plotted on a secondary y-axis.